

BRITISH SLUGS  
(PULMONATA ; TESTACELLIDAE,  
ARIONIDAE, LIMACIDAE)

BY  
H. E. QUICK



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## (PULMONATA; TESTACELLIDAE, ARIONIDAE, LIMACIDAE)

By H. E. QUICK

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## INTRODUCTION

No comprehensive work on British slugs has appeared since John William Taylor's classic monograph (1902-07). Besides full information on their nomenclature, systematics and biology, this contains excellent coloured plates, depicting numerous varieties of the eighteen species of slugs which he recognized as British. Besides much information on these species which has become available since 1907, five more species, a subspecies, and two aliens established in British greenhouses must be added to the list. Taylor omitted *Arion lusitanicus* (p. 135), although it had already been recorded from Britain, and it has since reappeared. *Milax budapestensis* (p. 160), another species of *Milax* provisionally referred to *M. insularis* (p. 156) and *Agriolimax caruanae* (p. 175) have been recorded; *Agriolimax reticulatus* (p. 164) has been shown to be specifically distinct from *A. agrestis*, and *Arion ater rufus* (p. 145) to be subspecifically distinct from *A. ater*. The alien species *Lehmannia poirieri* (p. 197) and *Limax nyctelius* (p. 202) have been found in Britain, but only in greenhouses. Two names used by Taylor must be changed: *Arion circumscriptus* to *A. fasciatus* (p. 127) and *Limax arborum* to *Lehmannia marginata* (p. 194).

Two more recent works also deal with all British slugs, though less completely. Ellis (1926) gives monochrome figures but only occasional references to internal anatomy; while Quick (1949) also gives monochrome figures, and information relating mainly to identification in the field. Among more general works, Kunkel (1916) on the biology of pulmonates, Økland (1923) on the Arionidae of Norway, and Boycott (1934) on the habits of British land molluscs may be especially mentioned. Much information on courtship and copulation is given by Gerhardt (1933, 1935, 1939 and 1940), on the seasonal abundance and growth of slugs in gardens and fields

by Barnes & Weill (1945, with good coloured plates of garden species), and on their ecology by Thomas (1944). For full synonymies, reference should be made to Kennard & Woodward (1926), and also to Taylor (1902-07) and Hesse (1926). Only the more important synonyms are quoted below.

The group of naked pulmonates termed slugs is highly polyphyletic in origin. British slugs belong to the three families Testacellidae, Arionidae and Limacidae, which have evidently been derived from shelled Oleacinids, Endodontids and Zonitids respectively.

### *Arrangement*

Information is given in the same sequence for each species (except that the shell is described before the external variations for *Testacella*) under the following headings, any of which may be omitted.

Notes	Radula
First British record	Alimentary system
Diagnostic features	Reproductive system
External appearance	Spermatophore
External variation	Mating
Shell	Development
Pallial organs	Behaviour
Pedal gland	Ecology
Retractor muscles	Distribution
Nervous system	Fossil record
Jaw	Material examined

The anatomical terms used in the descriptions are explained by means of a glossary and semi-diagrammatic figures on p. 203. Distributions in the British Isles are shown on vice-comital maps (p. 205), as well as being briefly described under "distribution".

### *Acknowledgments*

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## NATIVE AND NATURALIZED SPECIES

## Order STYLOMMATOPHORA

Pulmonate mollusca bearing eyes at the apex of retractile tentacles.

## Superfamily OLEACINACEA

Jaw rudimentary or absent, radular teeth aculeate, shell turreted or auriform. Carnivorous.

## Family TESTACELLIDAE

Shell small, auriform, situated at the posterior end of the body, covering the pallial organs. The upper tentacles (ommatophores) are not bulbous at the apex. There is no caudal mucus gland. A pair of lateral grooves with side branches directed obliquely upwards and forwards, and downwards and forwards, arises from a peripallial groove. The pedal mucus gland lies free in the body cavity. The cerebral commissure is very short, and the cerebro-pleural and cerebro-pedal commissures long. There is no jaw. The buccal bulb is enormous. The long narrow radular teeth, barbed at the apex, are disposed in transverse V-shaped rows, and a central tooth may be absent. The stomach is feebly developed and the anus lies just within the pulmonary cavity posteriorly. The kidney is without a secondary ureter. An osphradium is said to be present in a groove in the floor of the mantle cavity (Plate, 1891). The vagina is without accessory glands, and the right ocular retractor muscle passes forwards between the penis and vagina. *Testacella* is carnivorous, feeding on earth-worms and occasionally on other slugs, and is largely subterranean in habit.

Genus *TESTACELLA* Draparnaud, 1801

Type species *Testacella haliotidea* Draparnaud, 1801.

The sole genus, with the characters of the family. Through adaptation to a life spent largely underground, and a diet of earth-worms, the structure of *Testacella* has been profoundly modified. The relatively large shell and mantle cavity of other snails have been greatly reduced in size, and the body anterior to these structures elongated to accommodate the enormous buccal bulb with its powerful muscles and barbed radular teeth. The backwards shift of the pallial region is accompanied by a clockwise rotation of 180°, so that the heart and pericardium lie on the right side of the kidney with the ventricle in front of the auricle. The normal backwardly-directed loop of the intestine is obliterated, and the rectum runs backwards instead of forwards to the anus (beside the pulmonary orifice, at the rear).

It is convenient to gather together the available information on the life history of all the three British species of *Testacella*. A recent paper by Stokes (1958) gives further information, supplementing that of Barnes & Stokes (1951).

*Mating*

Little is known, but Gerhart (1940 : 579) reports that while unpacking a container he found a pair of *T. scutulum* in coitus in the moss, and accidentally separated them.



The penes were bluish-white, translucent, elongated, dorso-ventrally flattened cones, withdrawn from the adjacent vaginal openings. No appendix was visible, and the penes were of the simplest type occurring in land pulmonates. They quickly disappeared within the owners' bodies, and no more was to be seen. Barnes & Stokes (1951) found that the coitus of *T. haliotidea* and *T. scutulum* took place under the surface of the soil in their containers, the animals lying head to head: they do not mention any visible everted organs. Chemin (1939*a* and *b*) reports self-fertilization in *T. haliotidea* isolated when young.

### *Development*

The eggs are ellipsoidal, with a white calcareous shell which becomes yellow, and are laid underground. Those of the three British species are distinguished only by differences in size:  $5 \times 4$  mm for *T. maugei*,  $7 \times 4$  mm for *T. haliotidea*, and  $4 \times 3$  mm for *T. scutulum*. Barnes & Stokes confirm the old statement that they explode when placed on a warm hand. The eggs of *T. maugei* are laid in groups of 8–15 during the summer months, those of *T. haliotidea* and *T. scutulum* in captivity (Barnes & Stokes, 1951) in batches of 2–14 in March, 54–95 days after mating. Taylor (1902–07) records the time of development as 30–35 days for *T. maugei*, 20–36 days for *T. scutulum* and (quoting Gassies, 1840) 10–22 days for *T. haliotidea*. However, Barnes & Stokes found that embryonic development takes much longer than this for the latter two species: 144–201 days, or five to six months.

Like all our slugs and some, perhaps all, of the shell-bearing Stylommatophora except *Succinea* (which lacks a caudal vesicle), *Testacella* exhibits in the middle and late stages of development a haemocoelic cephalic vesicle protruding beneath the mantle over the head, containing part of the viscera; and a caudal haemocoelic vesicle projecting beyond the tail, which contains only haemocoelic fluid and corpuscles. The caudal vesicle varies in shape from genus to genus (see Text-fig. 18). In *Testacella* it is a flattened bilobed or broadly cordate sac (Text-figs. 1*D* and 18*C*). The two vesicles pulsate, expanding and contracting alternately so that haemocoelic fluid is driven back and forth, at a rate depending on the temperature. The vesicles may have an excretory or a respiratory function. The cephalic vesicle is withdrawn with its contents into the body, and shortly before hatching the caudal vesicle also shrinks and disappears. In *Testacella*, with its posterior mantle, the cephalic vesicle does not extend over the head (at any rate in the later embryonic stages).

### *Behaviour*

It has been noted (Adams, 1941) that dust sprinkled on *Testacella* leads to copious discharge of fluid which washes it away. Another phenomenon does not seem to have been recorded. When lightly irritated, *Testacella maugei* partially contracts, and sometimes a forcible discharge of air and froth occurs in the middle line from under the front of the mantle edge, with a distinct high-pitched hissing sound. Presumably a communication to the lung cavity exists, and air is expelled by closure of the pulmonary orifice and muscular contraction. No duct is apparent on gross dissection, but serial section of the area show spongy tissue leading to the anterior

expansions of the pulmonary cavity, through which air might be expelled. In its underground travels, or if dragged into a burrow by an attacked earth-worm, it is easy to imagine that earth could become impacted under the mantle border, and that the forcible expulsion of air and fluid would serve to dislodge it.

### *Ecology*

Mostly to be found in gardens, allotments and other cultivated ground. During the day *Testacella* remains underground, retreating deeper in dry weather but sometimes hiding under stones and herbage in damp weather; while at night it crawls freely on the surface. In the winter it hibernates in a strongly contracted state, in an underground cell. On slowly approaching a worm, the slug shoots out its radula and impales its prey at one end or in the middle, and engulfs it within a few minutes. Another worm may be eaten after a day or two. The faeces are very small in bulk and contain discarded radular teeth, fragments of worm cuticle and setae, and sometimes small white bodies which may be from the calcareous oesophageal glands of worms. *Testacella* is also said to eat other slugs.

### *Testacella maugei* Férussac, 1819

*Testacella maugei* Férussac, 1819: 94, pl. 8, figs. 10 and 12. Teneriffe.

*Testacella aurigaster* Watson, 1915: 221 (from Layard MS.).

### *Notes*

The type was found in 1796 by M. Maugé; who died before publishing an account. According to Turton (1831: 27), it was sent in 1812 from Dr. Leach at Bristol to Férussac. *T. aurigaster* refers to this species, introduced into South Africa (Watson, 1915: 221).

### *First British record*

By Férussac (1819).

### *Diagnostic features*

Pear-shaped appearance (body widest behind); shell large (14 × 7 mm); two median lines of dorsal tubercles conspicuous, especially in the young; lateral grooves wide (5 mm) apart at origin. Buccal bulb lacks lateral retractors; cephalic retractors arise asymmetrically, from left side. Penis swollen posteriorly, lacks the flagellum of *T. haliotidea*; penial retractor arises from body-wall about two-thirds of the way back; vas deferens convoluted near free oviduct; spermatheca duct long and slender, swollen proximally.

### *External appearance* (Pl. 1, fig. 13)

Length when extended, 6–10 cm. The most bulky part of the body lies behind the centre. The lateral grooves are separated by about 5 mm at their origin from the peri-pallial groove, and each gives rise to about fourteen dorsal and ventral

grooves directed obliquely forwards, which subdivide to produce the reticulate surface pattern. The row of tubercles on each side of the median dorsal line is more prominent than the other dorsal rows, especially in the young. The upper tentacles, bearing the small black eyes, are not bulbous at the apex, and the lower tentacles are short. The true pedal groove is only distinct for a few millimetres at the front of the foot fringe, but a peripodial groove above this runs to the tail. There is no caudal mucus gland. When crawling on a glass plate, the yellow sole is seen to be obscurely tripartite. The mucus is clear and viscid, drawing out into thin threads. The body is usually some shade of brown more or less sprinkled with darker spots, paler on the sides, and the sole is yellow or pink. The mantle is speckled with black, and the paler margin slightly overlaps the shell. The posterior respiratory orifice is bounded by the right and left mantle lobes.

#### *Shell* (Text-fig. 1 A)

The shell measures about  $14 \times 7$  mm, and has a brown periostracum, often abraded. It is more convex than the shells of the other two species, and the columella does not show the same callous enlargement at the hinder end. The crescentic muscle scar is visible on the under surface.

#### *External variation*

Variety *aperta* Taylor (1902) has the shell wider and flatter than normal. Varieties *albina*, *griseonigrescens*, *viridans* and *griseorubescens* Gassies & Fischer (1856), *nigra* Collinge (1898) and *aurea* Taylor (1902) are colour varieties, whose characteristics are suggested by their names.

#### *Pallial organs* (Text-figs. 2 D and F)

The respiratory cavity, bounded by the right and left mantle lobes, leads to the pulmonary chamber, which is bounded by spongy vascular tissue. Anterior to this, the chamber is prolonged forwards as thin-walled air sacs projecting into the visceral cavity. The somewhat quadrate kidney, opening without a secondary ureter at the back of the chamber, lies above and in front of the pulmonary chamber. The pericardium lies to the right of the kidney and the ventricle is anterior to the auricle, and both branches of the aorta run forwards. The rectum runs obliquely in the pulmonary chamber to terminate in the anus just above and on the left of the respiratory orifice. The kidney projects over the apex of the left liver lobe. An osphradium is represented by a ridge of cells in the floor of the respiratory chamber, and is innervated from the right visceral ganglion (Plate, 1891).

#### *Retractor muscles* (Text-fig. 1 E)

Both the cephalic retractor muscles arise from the body-wall on the left side. The right ocular retractor passes between the penis and the vagina, and a branch takes the same course to the side of the head. The slender penial retractor arises from the right body wall about two-thirds of the way back, and not from the posterior end as it does in *T. haliotidea* and *T. scutulum*.

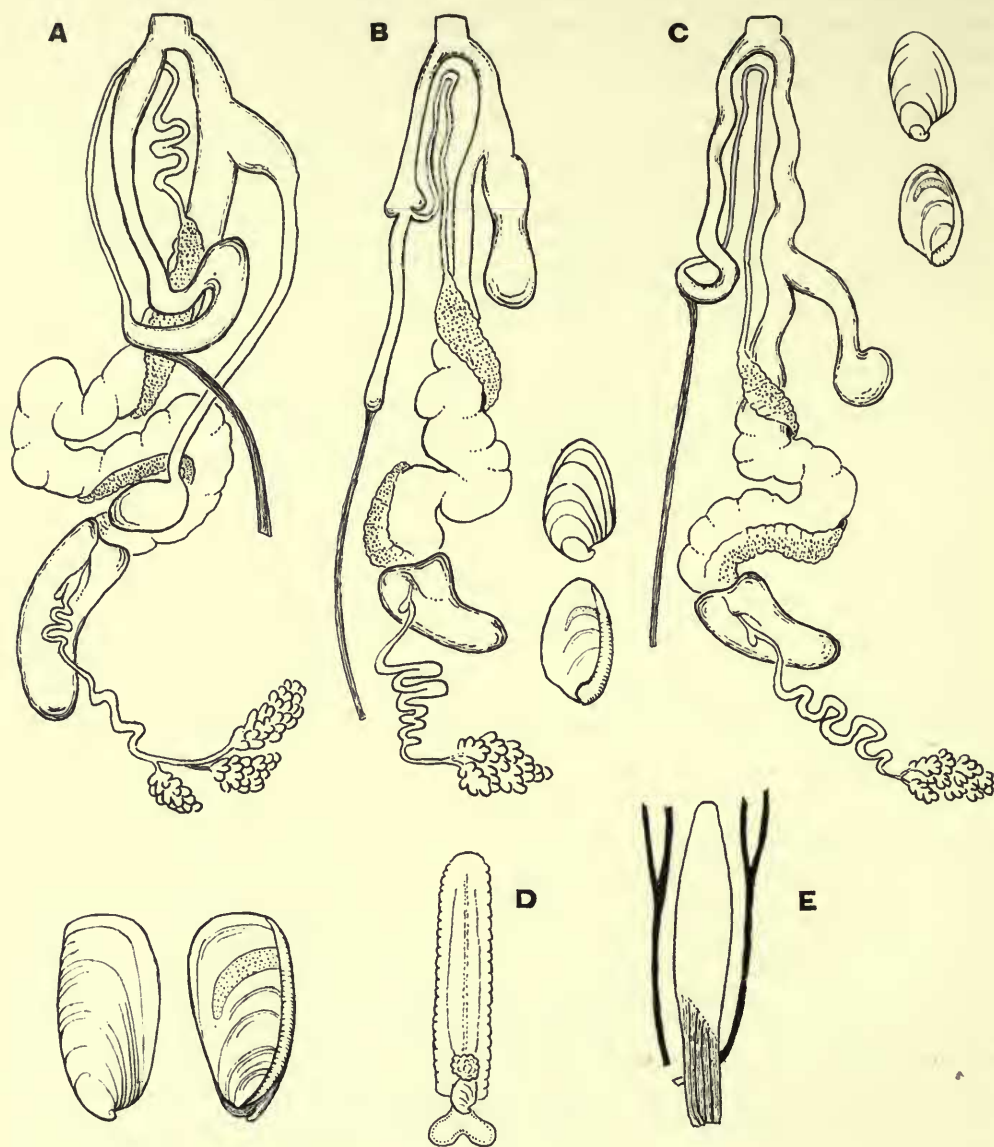


FIG. 1. *Testacella*. Reproductive organs ( $\times 3.3$ ), shell ( $\times 2$ ). A. *T. maugei*—shell below. B. *T. haliotidea*—shell right, below. C. *T. scutulum*—shell right, above.

D. *T. scutulum*—advanced embryo ( $\times 6.7$ ) showing cephalic vesicle in front of shell and caudal vesicle posteriorly. E. *T. maugei*—buccal bulb and ocular retractors.



*Nervous system* (Text-fig. 2 E)

The cerebral commissure is very short, and the cerebro-pleural and cerebro-pedal commissures are long to embrace the large buccal bulb. The buccal ganglia are large. The five visceral ganglia are close together, but not fused.

*Radula* (Text-fig. 2 A)

In each row, sixteen aculeate barbed teeth on each side of a small median tooth increase in size up to the penultimate one, while the sixteenth is much smaller. There are about fifty V-shaped rows.

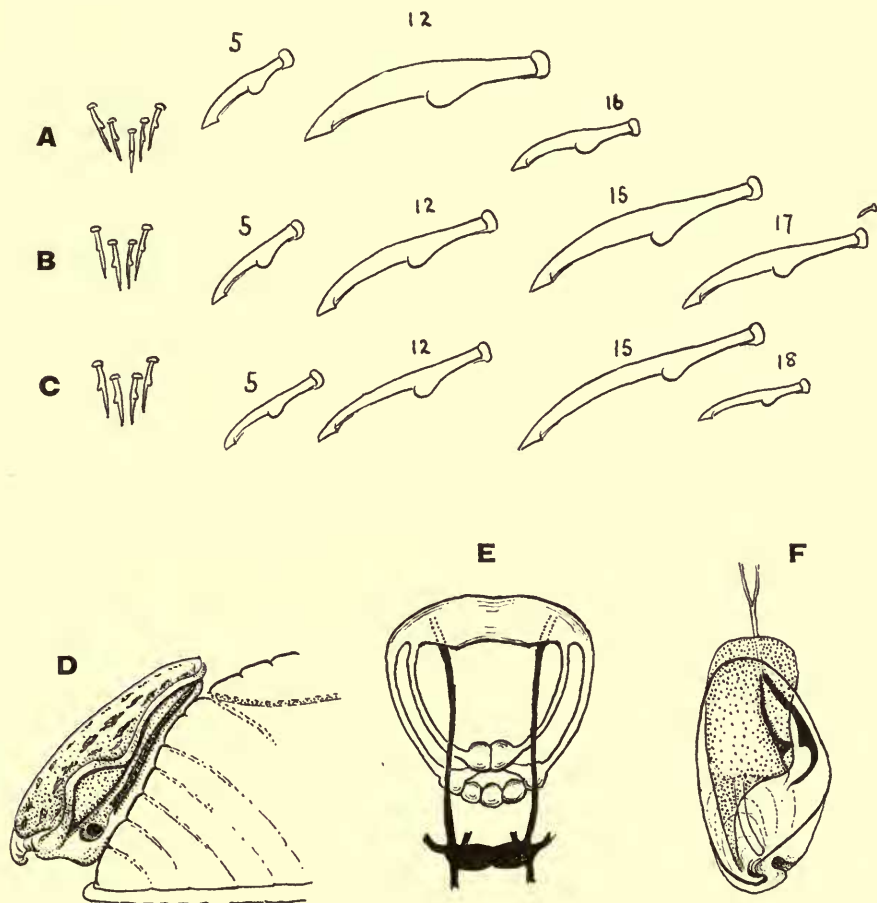


FIG. 2. *Testacella*. Representative radular teeth ( $\times 67$ ). A. *T. maugei*—showing central tooth. B. *T. haliotideae*—showing absence of central tooth. C. *T. scutulum*—showing absence of central tooth.

*T. maugei*. D. Posterior end of body ( $\times 3.3$ ) with shell removed and right mantle lobe reflected to expose respiratory orifice. E. Central nervous system, showing buccal ganglia (black) posterior to cerebral ganglia when animal is contracted. F. Pallial region, viewed as if shell were transparent.

*Alimentary system*

The buccal bulb, which is large but does not extend as far back as in *T. haliotidea* and *T. scutulum*, lacks lateral muscles but has a bundle of from two to four pairs of powerful muscles at the posterior end, attached to the diaphragm towards the left of the mid-line (Text-fig. 1 E). The small stomach is scarcely wider than the oesophagus and intestine. It receives the right and left liver ducts, and the left liver lobe forms the apex of the visceral mass. The intestine makes one forwardly-directed loop, and the long rectum runs backwards to the anus, close to the respiratory orifice.

*Reproductive system* (Text-fig. 1 A)

The reproductive organs are simple. The pale ovotestis lies at the apex of the visceral mass between the right and left lobes of the liver. The slightly sinuous hermaphrodite duct becomes slender and folded before entering the long narrow albumen gland, and bears a small seminal vesicle. The convoluted vas deferens, arising from the yellow ribbon-like prostate, runs forwards beside the free oviduct and then turns backwards, beneath the right ocular retractor to the apex of the penis. The penis is about 9 mm long, slender in front and dilated posteriorly and often folded over forwards. The mucous membrane is papillate at the apex and longitudinally ridged beyond, and there is no penial papilla. There is no caecum or flagellum. The penial retractor, arising from the right body wall about two-thirds of the way back, is inserted at the apex of the penis. The atrium is short and opens below the right upper tentacle. The free oviduct and vagina are wider than the penis. The long slender spermatheca duct is dilated at its origin from the oviduct, and enters the spermatheca sac laterally. The mucous membrane of the duct is longitudinally ridged, the ridges being more prominent in the bulbous part of the duct.

*Mating, Development, Behaviour, Ecology*

See pp. 108–110. The eggs measure  $5 \times 4$  mm.

*Distribution* (Map 1)

*T. maugei* is the most westerly of the three British species of *Testacella*, known from Tangier, south-western Spain, Portugal, Brittany, Dieppe and the Atlantic isles (and introduced into North America and South Africa). In England and Wales it occurs west of a line from Cheshire to Middlesex, and in Ireland south-east of a line from Dublin to Cork. It is probably truly native only in the south-west.

*Fossil record*

Holocene and Recent.

*Material examined*

Living specimens from Singleton Park Botanical Gardens, Swansea, Glamorgan. Spirit material from various British localities, the Azores and Madeira.

*Testacella haliotide* Draparnaud, 1801

*Testacella haliotide* Draparnaud, 1801 : 99. ? Montpellier.

*Testacella europea* de Roissy, 1805, 5 : 252.

*First British record*

By Lukis (1834), from Guernsey.

*Diagnostic features*

Less bulky posteriorly, when extended, than *T. maugei*; shell much smaller, ( $7 \times 5$  mm), columella somewhat truncate anteriorly, with conspicuous callous enlargement posteriorly; dorsal tubercles not especially prominent; lateral grooves close together at origin. Buccal bulb with powerful lateral retractors; cephalic retractors arise symmetrically. Radula lacks a central tooth, apophyses of marginal teeth nearly central. Penis with flagellum and short apical caecum; penial retractor arises from diaphragm at posterior end of body; spermatheca duct short and bulbous.

*External appearance* (Pl. 1, fig. 10)

Length when extended, 8–12 cm. The lateral grooves are close together at their origin from the peri-pallial groove. Colour usually dull greyish-yellow, with a pale sole and foot fringe.

*Shell* (Text-fig. 1 B)

Measures about  $7 \times 5$  mm, convexly auriform, triangular; brown periostracum usually much abraded. Columella usually slightly truncate anteriorly, and expanded to a rounded callus posteriorly.

*External variation*

In var. *trigona* Gassies & Fischer (1856) the shell is thicker and the right margin expanded, in var. *major* G. & F. the shell is larger ( $11.5 \times 7$  mm). The body is yellow in var. *flavescens* Moquin-Tandon (1855), and whitish in var. *albina* Moquin-Tandon.

*Pallial organs*

As in *T. maugei*.

*Retractor muscles*

The cephalic retractor muscles arise symmetrically on each side of the body-wall about two-thirds of the way back, and not from the left side only as in *T. maugei*. The long, slender penial retractor arises dorsally at the hind end of the body.

*Nervous system*

As in *T. maugei*.

*Radula* (Text-fig. 2 B)

The median tooth is vestigial or absent. On each side, eighteen barbed aculeate teeth gradually enlarge up to the penultimate one, while the eighteenth is shorter. The lateral apophysis is nearly midway between base and apex (especially towards the margin of the radula), while in *T. scutulum* it is nearer the basal end. There are about fifty V-shaped rows.

*Alimentary system*

The large buccal bulb is longer than in *T. maugei* and has, in addition to the bundle of posterior muscles attached to the diaphragm, a series of ten to fifteen pairs of lateral muscles attached to the posterior half of the bulb and arising from the left body-wall. The relations of the liver lobes, intestine and rectum are as in *T. maugei*.

*Reproductive system* (Text-fig. 1 B)

Compared with *T. maugei*, the central portion of the hermaphrodite duct is longer and more folded, the penis is slightly enlarged at the entrance of the vas deferens, and opposite this point there is a short blunt caecum. There is also a flagellum, which varies in length but may be two-thirds as long as the penis, from the apex of which a long slender retractor muscle runs to the diaphragm at the posterior end of the body. There is no penial papilla, and the mucous membrane is papillate. The spermatheca duct is short, wide and bulbous with the mucous membrane strongly folded longitudinally, and the sac is oval.

*Mating, Development, Behaviour, Ecology*

See pp. 108-110. The eggs measure  $7 \times 4$  mm, and so are considerably larger than those of *T. scutulum*.

*Distribution* (Map 2)

*T. haliotidea* is the most widely distributed species, ranging from the Atlantic isles to the Balkans, and from the North African coast to south Scotland. It probably occurs in every county in Britain up to Stirling, and in the south-eastern and southern counties of Ireland.

*Fossil record*

Holocene and Recent.

*Material examined*

Living specimens from Henley-on-Thames, Bedford and Cambridge. Spirit material from Britain, France and Majorca.

*Testacella scutulum* Sowerby, 1820

*Testacella scutulum* Sowerby, 1820 : pl. 159, figs. 3-6. Kennington Road, Lambeth, Surrey.

*Notes*

Taylor (1902-07) considers *T. bisulcata* Risso (1826) as a variety of this species. Plate (1891) and Hoffman (1925), however, consider it to be quite distinct. Plate's figure, copied by Hoffman, shows a flagellum from the anterior end of the penis, and a tubular connection from the vagina to the apex of the flagellum. This most unusual arrangement is said to be confirmed by serial sections.

*First British record*

By Sowerby (1820).

*Diagnostic features*

Resembles *T. haliotidea*, but differs in the following. Shell smaller ( $6 \times 3.5$  mm) and flatter; animal yellow in colour, speckled with brown. Apophyses of marginal radular teeth more basal. Penis lacks caecum and flagellum; free oviduct shorter than vagina; spermatheca duct longer and narrower (but quite different from that of *T. maugei*).

*External appearance*

Length when extended, 8-12 cm. The lateral grooves are said to be confluent for about 1 mm at their origin from the peri-pallial groove, but this does not seem to be constant. Colour some shade of yellow, more or less sprinkled with brown; sole and foot fringe brighter yellow.

*Shell* (Text-fig. 1 c)

Smaller than that of *T. haliotidea* ( $6 \times 3.5$  mm), and flatter—sometimes even concave. The brown periostracum tends to be retained better than in the other species. The columella is slightly truncate anteriorly and expanded posteriorly, as in *T. haliotidea*. Young shells of these two species can easily be confused.

*External variation*

Most of the varieties mentioned by Taylor (1902-07) refer to continental forms, which may or may not be conspecific with *T. scutulum*. However, var. *aurea* Cockerell (1885) presumably refers to this species: it is orange-coloured, with brown mottling and a bright orange foot sole.

*Pallial organs*

As in *T. maugei* and *T. haliotidea*.



*Retractor muscles*

The cephalic retractors arise symmetrically from the body-wall about half-way back. The penial retractor arises far back, from the diaphragm.

*Nervous system*

As in *T. maugei* and *T. haliotidea*.

*Radula* (Text-fig. 2 c)

As in *T. haliotidea*, the median tooth is absent and there are eighteen teeth on each side of the mid-line ; but in the outer marginal teeth the apophyses are nearer the bases. There are about forty-five V-shaped rows.

*Alimentary system*

The buccal bulb has three or four strong muscles from the diaphragm to its posterior end, and the hinder half has five to ten pairs of lateral muscles attached to the left body-wall. The relations of the liver lobes, intestine and rectum are as in *T. maugei* and *T. haliotidea*.

*Reproductive system* (Text-fig. 1 c)

The ovotestis, albumen gland, prostate and oviduct resemble those of *T. haliotidea*, but the free oviduct is relatively shorter and the vagina longer. The spermatheca duct is intermediate in length and breadth between those of *T. haliotidea* and *T. maugei*. The penis is cylindrical, without dilatations or flagellum, and the retractor muscle arises far back from the diaphragm. The penial mucous membrane is papillate, and that of the spermatheca thrown into longitudinal folds.

*Mating, Development, Behaviour, Ecology*

See pp. 108-110. The eggs are smaller ( $4 \times 3$  mm) than those of the other species, but otherwise similar.

*Distribution* (Map 3)

Taylor (1902-07 : 18) apparently treated *T. bisulcata* Risso (1826) as a variety of *T. scutulum*, so that his account of the latter's continental distribution is unreliable. In the British Isles, its distribution is almost the same as that of *T. haliotidea*.

*Fossil record*

Recent.

*Material examined*

Living specimens from Bedford. Spirit material from Britain and Corsica.

## Superfamily ENDODONTACEA

Shell spiral depressed, or reduced to a flat plate or mass of granules enclosed by the mantle. A supra-pedal groove is present, and a caudal mucus gland may be present or absent. The jaw is either crescentic and ribbed, or plaited. Marginal radular teeth generally aculeate. The genitalia are simple.

## Family ARIONIDAE

Slug-like animals with the mantle covering only the anterior part of the body, with the respiratory orifice in a slit on the right margin. Shell an oval plate or mass of granules except in *Binneya*, where it is exposed and spiral. The sole is uniform or tripartite. The kidney surrounds the pericardium. An epiphallus is present. The jaw is ribbed (odontognath), the central radular tooth tricuspid, lateral teeth bicuspid, marginals with short wide basal plates, with long mesocones and with or without ectocones.

The Arionidae require relatively high humidity, and dry barren areas are barriers to their dispersal. The family seems to have been derived from Endodontid stock with spiral shells, the cephalic and buccal retractor muscles with a common origin from the columella, and a penial papilla. In the primitive North American genus *Binneya*, the visceral hump is capped by a spiral *Vitrina*-like shell, the tail is solid and the retractors have a common origin. Various genera show transitions from this snail-like condition to that of the most modified subfamily, the Arioninae of the western Palaearctic Region. For a discussion of the probable evolution of the other subfamilies and genera, see Pilsbry (1948 : 660-665).

## Subfamily ARIONINAE

Slugs with a wide foot fringe ; caudal mucus gland present ; the shell is reduced to a flattened plate in *Geomalacus*, and to discrete granules in *Arion*. The cephalic retractor muscles are widely separated at their origin from the posterior border of the diaphragm. The stomach apex lies behind the posterior loop of the intestine. The ovotestis lies behind all the intestinal loops. There is no penis or vagina, and the oviduct, spermatheca and epiphallus enter the upper atrium separately.

Of the British genera, *Geomalacus* with its solid shell, anterior reproductive orifice, narrower foot fringe, and extreme western distribution, seems to be the more primitive.

Genus *GEOMALACUS* Allman, 1843

Type species *Geomalacus maculosus* Allman, 1843.

Genital orifice below and behind the right upper tentacle ; atrium greatly elongated ; genital retractor muscle arising from the dorsal body-wall at the extreme posterior end of the body and inserted into the spermatheca duct ; shell a compact oval calcareous mass.

*G. maculosus* is the only member of this genus occurring in the British Isles, though one or two more are found with it in the Iberian peninsula.

***Geomalacus maculosus* Allman, 1843**

*Geomalacus maculosus* Allman, 1843 : 851. Lough Caragh, Co. Kerry, Ireland.

*Notes*

The types were found by W. Andrews of Dublin in 1842.

*First British record*

By Allman (1843).

*Diagnostic features*

Distinguished from species of *Arion*, externally by the anterior situation of the reproductive orifice, narrower median area of the sole, and maculate colour pattern ; and internally by the solid oval shell, greatly elongated atrium, and long genital retractor arising far back from the mid-dorsal line of the body-wall.

*External appearance* (Pl. 1, fig. 1)

Length when extended about 5.5 cm, but occasionally up to 9 cm. The granulose mantle occupies about one-third of the body, with the respiratory orifice a little in front of the centre of the right border. The reproductive orifice is nearer to the right upper tentacle than to the respiratory orifice. The supra-pedal groove is deep and distinct and the pedal groove indistinct. The caudal mucus gland is a transverse slit. The body shows about twenty-five rows of polygonal tubercles (Text-fig. 3 c). The colour is grey, brown or nearly black, irregularly marked with yellow or white maculations more or less developed. The young have two longitudinal bands on each side, which tend to become obscured in the adult, but sometimes remain. In contrast to *Arion*, *Geomalacus* sometimes rolls up like the woodlouse *Armadillidium*.

*External variation*

Var. *fasciata* Cockerell (1892) retains the banding characteristic of the young—animal white or whitish with black or brown markings : mantle with dark marbling and lateral bands, body with a dark subdorsal band along each side. Charles Oldham bred in captivity a crimson form, var. *rutilans* Oldham (1942b), which has not been observed in the wild. The other varieties depend merely on the relative development of dark pigment on a pale ground : var. *allmani* Heynemann (1873), dark brown or grey with whitish maculations ; var. *verkruzeni* Heynemann, grey, darker dorsally, with whitish maculations ; var. *andrewsi* Mabile (1867), whitish, overspread with blackish spots.



*Shell* (Text-fig. 3 I)

Variable, but usually solid, oval, convex above and concave below, measuring about  $4 \times 3$  mm.

*Pallial organs* (Text-fig. 3 B)

The kidney completely surrounds the pericardium, and the cavity is occupied by lamelliform folds. The ventricle lies behind the auricle. The anterior branch of the aorta follows the usual course, arching over and passing beneath the anterior intestinal loop, and running forwards between the visceral and pedal ganglia to supply the anterior end of the body. The posterior aorta runs backwards to the digestive and genital systems.

*Retractor muscles* (Text-fig. 3 B)

The right and left cephalic retractor muscles are widely separated at their origin from the diaphragm, behind the kidney. The buccal retractor arises from the dorsal body-wall, a little further back and slightly to the right of the middle line. The right tentacular branch lies to the left of the oviduct and epiphallus, and does not pass between them.

*Nervous system*

The cerebral commissure is of medium length. The cerebral ganglia give rise to nerves to the head and lips, the peritentacular nerves, the combined ocular and olfactory nerve, the nerve to the lower tentacle, and on the right side to the genital nerve supplying the epiphallus and vas deferens. The right pleural, visceral and abdominal ganglia are fused together, but just distinguishable, and the same is true of the left pleural and the left visceral ganglia. The pleuro-pedal commissures are very short. The buccal ganglia, as well as supplying the buccal bulb, send a nerve to the salivary glands.

*Jaw* (Text-fig. 3 D)

The jaw is about 3 mm across, dark brown, arcuate, and crossed by eight or ten broad ribs which slightly denticulate the upper and lower margins. The number of ribs may be reduced by fusion, and there is sometimes a slight median projection.

*Radula* (Text-fig. 3 E)

The radula is about 8 mm long. There are usually about 200 rows of teeth, but the number varies considerably. The central tooth has very small ectocones. The lateral teeth, about twenty in number, have a large mesocone, a small ectocone, and no endocone. The ectocone gets smaller in the outer lateral teeth. In the marginal teeth it descends to the base of the mesocone, and gets larger again as the margin of the radula is approached.

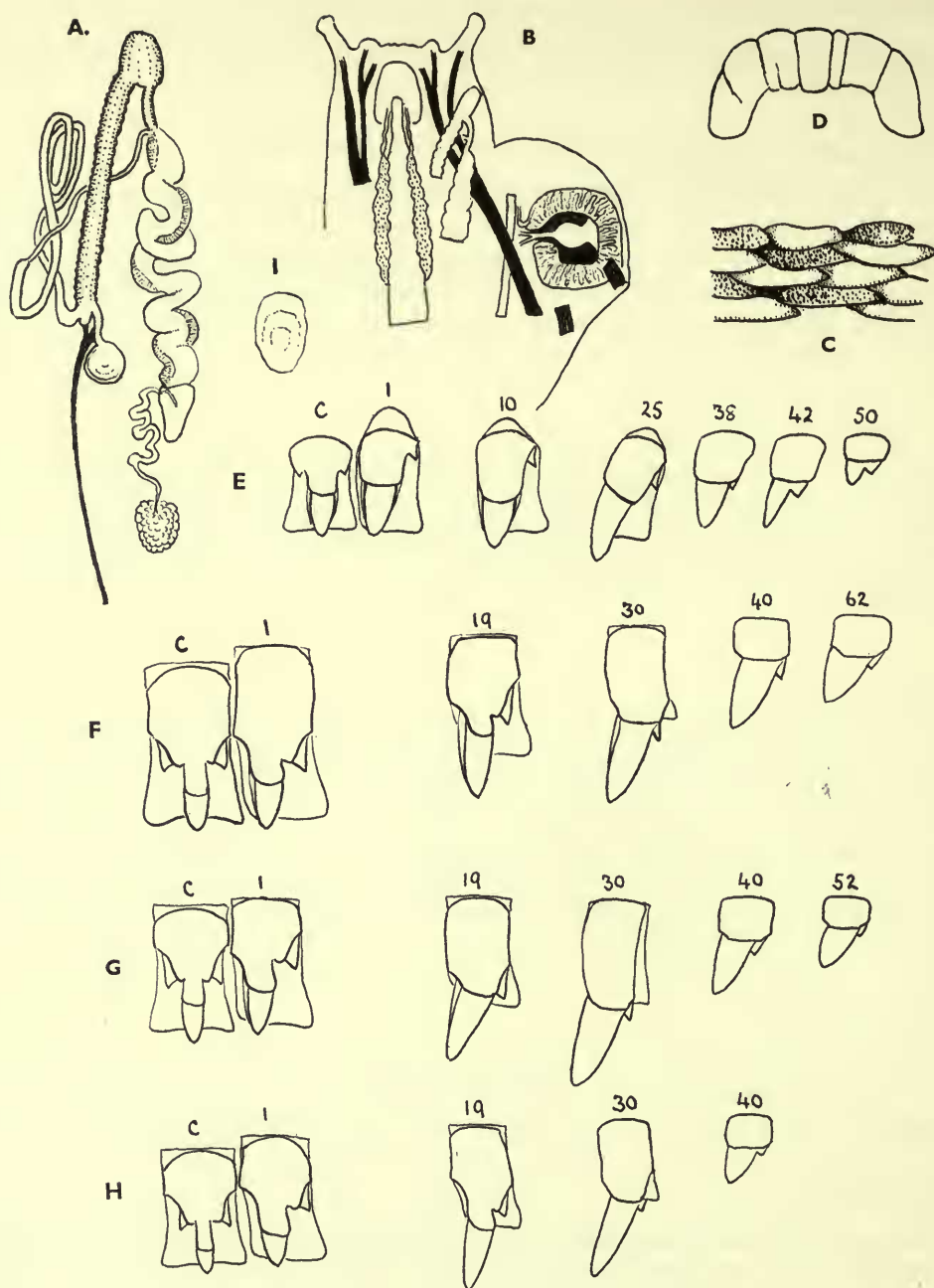


FIG. 3. *Geomalacus maculosus*. A. Reproductive organs ( $\times 2.7$ ). B. Head and mantle region ( $\times 1.7$ ) with mantle reflected to the right showing kidney, pericardium, rectum, terminations of genital and alimentary systems, origin of pharyngeal and left ocular retractors cut short. C. Polygonal body-tubercles. D. Jaw ( $\times 13$ ). E. Representative radular teeth ( $\times 330$ ). I. Shell. *Arion*. Representative radular teeth ( $\times 330$ ). F. *A. ater*. G. *A. lusitanicus*. H. *A. subfuscus*.

### *Alimentary system*

The oesophagus, after passing through the nerve ring, enlarges to a crop, merging into the stomach which forms the most posterior part of the alimentary canal. The narrower intestine passes far forwards (to the level of the kidney) and then turns back, but does not reach the stomach before it runs forwards again, as the rectum, to end in the anus in the posterior lip of the respiratory orifice. The short ducts of the anterior and posterior lobes of the liver open at the junction of stomach and intestine.

### *Reproductive system* (Text-fig. 3 A)

The somewhat raspberry-shaped brown ovotestis lies between the upper and lower lobes of the liver, at the apex of the stomach. The pale hermaphrodite duct passes forwards, becoming wider and folded, towards the linguiform albumen gland. It then becomes narrower, runs backwards between the lobes of the albumen gland, and turns sharply forwards, forming a "claw" or seminal vesicle. The common duct is much folded, the prostatic portion showing as a yellow ribbon. The narrower free oviduct enters the lower end of the atrium; its mucous membrane is thrown into fine longitudinal folds. The lower atrium shows internally a complicated mass of large sinuous folds, and is also remarkable in having a long slender diverticulum with circular folds, extending backwards as far as the albumen gland. The short duct of the globular spermatheca enters the apex of this diverticulum. The vas deferens runs backwards from the free oviduct towards the apex of the atrial diverticulum, to enter the wider epiphallus which is very long and much coiled, the coils being bound together by connective tissue. The epiphallus enters the atrial diverticulum close to the spermatheca duct. A long slender retractor muscle, arising from the mid-dorsal line at the posterior end of the body, is inserted at the neck of the spermatheca and apex of the diverticulum. The mucous membrane of the epiphallus shows longitudinal rows of papillae, and that of the spermatheca longitudinal folds. A membrane with a series of muscular bands extends from the atrial diverticulum to the diaphragm, and similar bands from the lower atrium to the body-wall.

### *Mating*

This has not been recorded.

### *Development*

The ellipsoidal eggs are said (Taylor, 1902-07 : 256) to be relatively large, from  $8.5 \times 4.25$  to  $6 \times 4$  mm, and to be white when laid, turning brown. They are laid, in clusters of from 18 to 24, in July and August, and hatch in from six to eight weeks. The young, which mature in the following summer, show two dark bands on each side which fade during growth.

### *Behaviour*

When irritated, it can roll up like the woodlouse *Armadillidium* (Taylor, 1902-07 : 257).

*Ecology*

*G. maculosus* lives on the bare mountain slopes of Old Red Sandstone in Cork and Kerry, where it browses on the algae, mosses and liverworts which coat the boulders. In captivity it readily feeds on lettuce and carrot, and has been observed to attack small snails such as *Vitrina pellucida*.

*Distribution* (Map 4)

Portugal, north-western Spain, and Vennes (France). In Britain it is confined to south-western Ireland, in the counties of Cork and Kerry.

*Fossil record*

Recent.

*Material examined*

Preserved specimens from Glengariff, Co. Cork (August 1931), and other localities in Cork and Kerry.

Genus **ARION** Férussac, 1819

Type species *Arion empiricorum* Férussac (= *Limax ater* Linnaeus, 1758).

The diagnostic features of the genus are those of the subfamily Arioninae. Differences from *Geomalacus* are: reproductive orifice immediately below posterior lip of respiratory orifice; upper atrium not prolonged backwards as a diverticulum; genital retractor short, arising from diaphragm close to left cephalic retractor, and inserted into both spermatheca duct and free oviduct; shell reduced to discrete granules; median area of sole wider.

*A. intermedius* and *A. fasciatus* seem to be less advanced than the other species, in the absence of a ligula, the limited eversion of the genitalia during coitus (in *A. fasciatus* at least), and the slightly more anterior position of the reproductive orifice in *A. fasciatus*. *A. hortensis* differs strikingly from *A. fasciatus* and from the larger species, but agrees with *A. subfuscus* and *A. lusitanicus*, in having the ligula (or its functional equivalent) in the proximal part of the oviduct. *A. lusitanicus* is in some respects intermediate between *A. subfuscus* and *A. ater*; while the latter, in which the banding pattern disappears completely in the adults, is probably the least primitive.

The various subgenera and sections that have been proposed are not satisfactorily delimited. Hesse (1926: 64-69) uses the following subgenera: *Lochea* Moquin-Tandon (1855), for *A. ater* and *A. lusitanicus* (though the genitalia of the latter are much more like those of *A. subfuscus*); *Mesarion* Hesse, for *A. subfuscus*; *Carinarion* Hesse, for *A. fasciatus*; *Kobeltia* Siebert (1873), for *A. hortensis*; and *Microarion* Hesse, for *A. intermedius*.

*Arion intermedius* Normand, 1852

*Arion intermedius* Normand, 1852 : 6. Valenciennes.

*Arion minimus* Simroth, 1885 : 237, pl. 7, fig. 41.

*First British record*

By Alder (1848 : 124), as *Arion flavus*.

*Diagnostic features*

Small size, tubercles assume a conical shape with translucent apices when animal contracts, yellow mucus accumulates at each end of foot ; reproductive orifice slightly anterior to respiratory orifice.

*External appearance* (Pl. 1, fig. 7)

This is the smallest British Arionid, about 2 cm long when crawling. Its colour varies from yellow to some shade of grey, with the head darker grey or black, and there may or may not be body and mantle bands. All these colour varieties may be found living together. *A. intermedius* is easily distinguished from the young of larger species by the form of its tubercles, which stand up in little conical eminences with translucent tips when the animal contracts—hence the popular name Hedgehog Slug. The pair of mantle bands together form a lyre-shaped figure, and the right band arches over the respiratory orifice and sends a branch down below and behind it. The sides of the body are paler than the back, the foot fringe is yellowish-grey, and just above it there is a row of black dots towards the anterior end. The sole is yellowish-grey, and yellow mucus tends to accumulate at each end of it. The genital orifice is immediately below the slit of the respiratory orifice, and thus is further back than in *A. fasciatus* but slightly further forward than in the other species.

*External variation*

Var. *normalis* Moquin-Tandon (1855), yellow with blackish head and tentacles ; var. *plumbea* Collinge (1892b), dark grey ; var. *brunnea* Taylor (1902-07), maroon-brown with darker bands ; var. *alba* Taylor, almost white.

*Shell*

The shell granules are not specifically distinguishable. In calcareous sites they may be aggregated into an irregular mass.

*Pallial organs*

As in *A. ater* (p. 139).

*Retractor muscles*

As in *A. ater*, except that the cephalic retractors do not arise at the same level, but with the right a little further forward than the left ; while the genital retractor



sends a branch to the junction of oviduct and atrium, as well as to the neck of the spermatheca.

#### *Nervous system*

As in *A. ater*.

#### *Jaw*

About 1 mm across, arcuate and crossed by seven to ten widely-spaced ribs. Of the usual Arionid shape, and so not like Taylor's figure (1902-07, fig. 248).

#### *Radula*

About 2 mm long, with about 120 transverse rows of teeth. The base of the mesocone of the central tooth is more constricted than in the other species. There are about sixteen lateral and sixteen marginal teeth, each with mesocone and ectocone: they do not have endocones. Formula C.16.16  $\times$  120.

#### *Alimentary system*

As in *A. ater*, except that the visceral mass is less twisted.

#### *Reproductive system* (Text-fig. 4 H)

The deeply pigmented ovotestis lies between the lobes of the liver, and is partly exposed on the surface of the visceral mass. The central part of the pale hermaphrodite duct is wider and somewhat sinuous, then narrows and runs back on the short linguiform albumen gland and bends sharply forwards, making a "claw" or seminal vesicle. The sperm-oviduct is short, and the free oviduct enters the very short upper atrium without a ligula. The mucous membrane is thrown into five or six low longitudinal folds. The lower atrium is about 2 mm long and smooth internally. The spherical spermatheca is connected to the upper atrium by a very short duct, much dilated at its base. The vas deferens is about 2 mm long, and the epiphallus about the same length.

#### *Spermatophore*

Unknown.

#### *Mating*

Not recorded.

#### *Development*

The ellipsoidal eggs are relatively large ( $2 \times 1.5$  to  $2 \times 2$  mm), opaque, white and dotted with calcareous spots. They are laid in the summer and autumn, and hatch in about three weeks. The young at birth are 4 mm long, and easily recognizable as miniatures of the adults.

*Ecology*

Common in the moist ground-litter of woods and copses, beneath logs, and at the roots of grass in open fields. Often found feeding on toadstools in the wild, and in captivity readily eats carrot, lettuce and oatmeal.

*Distribution* (Map 5)

Portugal, Spain, France, northern Italy, Switzerland, Germany, Scandinavia, Russia, Azores (and introduced into New Zealand, Polynesia and North America). It probably occurs in every vice-county in the British Isles, including islands northwards to the Orkneys and Shetland.

*Fossil record*

Although shell granules of *Arion* are not recognizable with certainty, they are recorded from the Cromerian onwards. They cannot be assigned specifically.

*Material examined*

Living specimens from many parts of England and Wales. Spirit material from Britain, France, Norway and Tahiti.

*Arion fasciatus* (Nilsson, 1822)

*Limax fasciatus* Nilsson, 1822 : 4. ? Sweden.

*Arion circumscriptus* Johnston, 1828 : 76.

*Notes*

Collinge (1892*b*) reinstated Nilsson's name, though it has not been adopted by other British authors. Lohmander (1937) also concluded that *fasciatus* is the valid name, though he continued to use *circumscriptus*. Nilsson's description of his species leaves no doubt that it is the *A. circumscriptus* of most authors, and Collinge's use of *fasciatus* prevents any action being taken to conserve *circumscriptus*.

*First British record*

By Johnston (1828).

*Diagnostic features*

Body bell-shaped in transverse section when contracted, mid-dorsal line of tubercles pale and raised, reproductive orifice in front of respiratory orifice, right mantle band arches over respiratory orifice, sole opaque porcelain white ; spermatheca with short stout duct and long tapered sac, spermatophore coiled anteriorly.

*External appearance* (Pl. 1, fig. 5)

Length when crawling about 3–3.5 cm. Easily distinguished from *A. hortensis* by the opaque white sole, and by the bell-shaped transverse section of the body

when contracted (caused by splaying-out of the lower part). The reproductive orifice is further forward than in our other species, being a little in front of the slit of the respiratory orifice. Body and mantle some shade of grey, becoming paler towards the foot and with a dark lateral band on each side. The mantle bands form a lyre-shaped figure, and the right band arches over the respiratory orifice without sending a branch below it. The bands are set at a higher level than in *A. hortensis*. The tubercles of the mid-dorsal line are larger and paler than those on each side, forming a keel (hence the sectional name *Carinarion* Hesse, applied to this species) : this is often more distinct in the young. The foot fringe is somewhat lineolated, especially towards the tail.

### *External variation*

Var. *grisea* Collinge (1892c), light silver-grey with dark bands ; var. *flavescens* Collinge (1892a) (= var. *circumscripta* Økland, 1923), light brownish-yellow, with dark bands and a yellow zone over the foot. Lohmander (1937) discusses whether these and other named forms are varieties or subspecies.

### *Pallial organs*

As in *A. ater*.

### *Retractor muscles*

The genital retractor is mainly inserted into the duct of the spermatheca, but usually sends a small branch into the middle of the free oviduct. Otherwise as in *A. ater*.

### *Nervous system*

As in *A. ater*.

### *Jaw*

Of the usual arcuate shape, crossed by ten to twelve ribs ; about 1.25 mm across, coloured yellow to pale brown.

### *Radula*

Closely resembles that of *A. hortensis*, but the marginals often have the small ectocone better developed. Length 3-4 mm, formula C.11.23  $\times$  120.

### *Alimentary system*

As in *A. ater*, except that the visceral mass is less twisted.

### *Reproductive system* (Text-fig. 4 1)

The ovotestis is darkly pigmented, the hermaphrodite duct has the usual "claw" or seminal vesicle at its entry into the albumen gland, and the sperm-oviduct is pinkish in colour, with a broad yellow prostatic ribbon. The free oviduct is rather



long and slender, agreeing with that of *A. intermedius* in not being dilated terminally to contain a ligula as in *A. hortensis*. The spermatheca has a short stout duct and an elongated sac, wide at the base and tapering apically. It varies a good deal, sometimes assuming bizarre shapes. The vas deferens is about the same length as the epiphallus, which terminates with a slightly marked annular swelling. The upper atrium is very small, and contains no ligula. The lower atrium is long, dorso-ventrally flattened, and yellow.

#### *Spermatophore* (Text-fig. 4 G)

A chitinous tube about 4 mm long, with five low ridges of which the most prominent is finely toothed. Within the spermatheca, the spermatophore is bent into a U, and is swollen for a short distance behind the slender coiled anterior end. On this swollen part, Lohmander (1937) describes, but does not figure, a small projection which anchors the spermatophore to the mucous membrane of the spermatheca. Økland (1923) figures an incomplete spermatophore, and Lohmander (1937) complete ones.

#### *Mating*

Coitus lasts about twenty minutes. In contrast to *A. hortensis*, *A. subfuscus* and *A. ater*, there is little or no eversion of the genitalia.

#### *Development*

The ellipsoidal eggs,  $3 \times 2$  mm, are yellow or sometimes dark amber, more flexible and translucent than those of other species of *Arion*. They are laid in clutches of up to thirty, from May to the autumn, and hatch in four or five weeks (or longer in cold weather). The newly-hatched young are 5 mm long, pale yellowish-grey; not darker dorsally, but with a pale central line of larger tubercles forming a keel towards the tail. The lyre-shaped figure formed by the mantle bands is faint in front and darker posteriorly.

#### *Ecology*

*A. fasciatus* is common amongst dead leaves and moss and under logs and stones, in thickets, fields and waste places, and sometimes in gardens.

#### *Distribution* (Map 6)

Probably every vice-county of the British Isles, and in Iceland (? introduced), the Faroes, Scandinavia, France, northern Italy, Rumania, western Russia, ? Spain. Introduced into North America.

#### *Material examined*

Living from many places in Britain. Spirit material from Britain, France and Italy.

*Arion hortensis* Férussac, 1819

*Arion hortensis* Férussac, 1819: 65, pl. 2, figs. 4-6. Presumably France.

*Arion elongatus* Collinge, 1894: 66, pl. 5A, figs. 1-4.

*Arion coeruleus* Collinge, 1897b: 444.

*First British record*

By Gray (1821: 239).

*Diagnostic features*

Differs from *A. fasciatus* in the following: body semicircular in transverse section when contracted, no enlarged mid-dorsal tubercles, reproductive orifice further back, mantle band surrounds respiratory orifice, sole yellow or orange; spermatheca globular, free oviduct longer and proximally more slender, spermatophore hooked posteriorly and either discoidal or pointed anteriorly, brown patch on buccal bulb.

*External appearance* (Pl. 1, fig. 4)

Length extended 2.5-3 cm. When contracted, the body is semicircular, not bell-shaped, in transverse section. The reproductive orifice is below the posterior lip of the respiratory orifice. The dark brown or black back is sprinkled with yellowish-brown dots, giving a pepper-and-salt appearance, the sole is pale yellow to bright orange, and the mucus is yellow. In alcohol, the back becomes bluish-grey and the sole loses its orange colour. The lateral bands are placed lower on the body than in *A. fasciatus*, and run along the edges of the mantle, surrounding the respiratory orifice instead of arching over it.

*External variation*

Var. *grisea* Moquin-Tandon (1855), pale grey and bandless; var. *nigra* Moquin-Tandon, bands nearly obliterated by general dark pigmentation; var. *rufescens* Moquin-Tandon, reddish with black bands; var. *caerulea* Collinge (1892a), bluish with dark bands, and yellow sides.

*Pallial organs*

As in *A. ater*.

*Retractor muscles*

As in *A. fasciatus*.

*Nervous system*

As in *A. ater*.

*Jaw* (Text-fig. 7 G)

About 1 mm across, doubtfully distinct from that of *A. fasciatus*.

*Radula*

Similar to that of *A. fasciatus*, but the ectocone of the marginal teeth is less frequently present. Formula C.II.24  $\times$  100.

*Alimentary system* (Text-fig. 4 A)

Visceral mass less twisted than in *A. ater*. The buccal bulb has a brown shield-shaped mark on the upper surface—an apparently good specific character not recorded in the literature.

*Reproductive system* (Text-figs. 4 B and C)

The very darkly pigmented ovotestis lies over the apex of the stomach, near the posterior end of the visceral mass, and is largely exposed on the surface. The middle dilated portion of the hermaphrodite duct is much folded, yellowish-white, and the terminal slender part shows the usual "claw" or seminal vesicle where it enters the elongated albumen gland. The sperm-oviduct is pale pinkish-brown, with a conspicuous yellow ribbon-like prostate. The free oviduct is unusually long and slender proximally, and dilated distally before entering the small white upper atrium. The vas deferens is short, and the epiphallus about the same length. The spermatheca duct is short and stout, with a bulbous base, and the sac is spherical. The lower atrium is yellow, with a soft glandular covering.

As in *A. fasciatus* and *A. intermedius*, there is no ligula in the upper atrium. However, within the dilated distal end of the oviduct (Text-fig. 4 C), two conspicuous longitudinal folds correspond functionally with this structure during coitus (Quick, 1946). Below the termination of the spermatheca duct is a region of thickened mucous membrane in the atrium. In the slugs observed in Swansea (see below), the entering spermatophore adhered to this region. The epiphallus terminates in a short papillate papilla, which is very conspicuous when the atria are everted in coitus (Text-fig. 4 E).

Both British and Dutch slugs show some variation in the folds of the oviduct representing the ligula, and in the relative length and thickness of the firm cartilaginous part; but these differences could be due to differences in the degree of maturity of the animals, and to the extent of contraction during fixation in alcohol.

*Spermatophore* (Text-figs. 4 F and M)

Two types of spermatophore have been found in slugs from different localities. Since the spermatophores of *Arion* are seldom seen, it seems better to regard the slugs bearing the two types as varieties or local races, rather than as distinct species, until further anatomical or ecological differences are demonstrated.

Slugs from Reading and from Zaandam in Holland (collected by Mr. D. Aten) have spermatophores in the form of simple chitinous tubes, 6.5 mm long, recurved at the slender posterior end and slightly shouldered near the anterior end, smooth and without denticulation (Text-fig. 4 F).

Slugs from a garden in Eaton Crescent, Swansea (Glamorgan), which otherwise agree with those from Reading, have the very different spermatophores described

by Quick (1946). These are 5 mm long, shaped like cloves, with the anterior end forming a flattened disc with a crenulated edge, and with a ridge carrying about fifty-six forwardly pointing denticulations running the whole length of the convex side (Text-fig. 4 M).

#### *Mating* (Text-fig. 4 D)

Mating occurs in April and December, and probably in other months. After the usual "following" and licking of mucus, slugs from Swansea (spermatophores as in Text-fig. 4 M) curve in a semicircle head to head, and the atria are everted as a translucent mass with the lower atria stretched to a narrow yellow ring and the lower atria in contact. A long slender mobile club-shaped process is everted, which plays over the partner's body in the same manner as the sarcobelum of *Agriolimax*. However, subsequent dissection shows it to be the everted slender proximal part of the oviduct, functioning as a stimulatory organ, a modification which appears to be unique (Text-fig. 4 E).

Coitus in Swansea slugs lasts for about an hour and a half. Gerhardt (1935) describes the mating of *A. hortensis* as lasting only twenty-five minutes, and the everted masses as small and featureless, in slugs whose spermatophores lacked serrations. This suggests that more than one species may be involved, though Mr. D. Aten (*in litt.*) states that the Zaandam slugs, having smooth spermatophores, evert their oviducts in coitus.

#### *Development*

The opaque yellow, sticky eggs measure  $2.5 \times 2$  mm, and are laid in clusters of up to thirty. A second and third clutch may follow at three-weekly intervals. In the winter, the eggs take six or seven weeks to hatch. The newly hatched young are 4 or 5 mm long, and differ from those of *A. fasciatus* in having a darker dorsum and central mantle area. The usual body bands and lyriiform mantle bands are present, and there is no dorsal line of pale conspicuous tubercles. The tentacles are violet-brown.

#### *Ecology*

This species is very common in gardens, allotments and fields, and burrows in the ground more than the other species of *Arion*. It can become a serious pest, by eating carrot, potato, etc. It is also frequent in woodland under logs and débris.

#### *Distribution* (Map 7)

Every county in the British Isles; Scandinavia and western Europe to western Russia, (North Africa). Introduced into North America.

#### *Material examined*

Living and in spirit from many places in England and Wales, and from Zaandam, Holland.

*Arion subfuscus* (Draparnaud, 1805)

*Limax subfuscus* Draparnaud, 1805 : 125, pl. 9, fig. 8. France.

*Arion fuscatus* Férussac, 1819 : 65, pl. 2, fig. 7.

*First British record*

Possibly by Johnston (1838), as *Arion subflavus* (a nomen nudum). Up to about 1880, however, *A. subfuscus* was generally considered as a variety of *A. ater*.

*Diagnostic features*

Adults larger (6–7 cm) than *A. fasciatus* and *A. hortensis*, smaller than *A. lusitanicus* and *A. ater*; differ from young of large species in smaller tubercles, narrower foot fringe, inability to contract to hemispherical shape. Internally differs from *A. hortensis* in relatively shorter proximal, slender, part of free oviduct, longer spermatheca duct.

*External appearance* (Pl. 1, fig. 2)

Length extended, from 5 to 7 cm. The colour is usually yellowish-brown, darker on the dorsum and head and on the body bands. On the mantle the right band completely surrounds the respiratory orifice. The foot fringe is yellowish and lineolated more or less distinctly with black, and the sole is pale yellow, sprinkled with whitish specks, and obscurely tripartite. The mucus, especially on the mantle, is yellow or orange. When contracted, *A. subfuscus* neither assumes the hemispherical shape nor exhibits the rolling reflex (p. 145) of *A. ater*.

*External variation*

This as usual depends on the relative development of black, red and yellow pigment, and the distinctness of the bands: var. *rufofusca* Draparnaud (1805), rufous with black bands; var. *bicolor* Moquin-Tandon (1855), red with darker dorsum and no bands, foot fringe orange; var. *fuliginea* Morelet (1845), dark brown, fringe yellowish; var. *nigricans* Pollonera (1887b), black; var. *cinereofusca* Draparnaud (1805), ashy grey; var. *succinea* Bouillet (1835), yellow or orange; var. *pegorarii* Lessona & Pollonera (1882), quadrifasciate; var. *alba* Esmark (1883), whitish. In most cases, the yellow pigment is largely contained in the mucus, and when this is removed the animal becomes brown or grey, as do alcohol specimens.

*Pallial organs, retractor muscles, nervous system*

As in *A. ater*.

*Jaw*

Brown, arcuate, about 1.5 mm across, with from ten to sixteen transverse ribs.



*Radula* (Text-fig. 3 H)

About  $4.5 \times 2$  mm. About ten more teeth on each side of each row than in *A. hortensis*. Formula C.15.30  $\times$  140.

*Alimentary system*

Similar to that of the other species of *Arion*, except that the visceral mass is rather more twisted than in *A. intermedius* and *A. fasciatus*, and less so than in *A. ater*.

*Reproductive system* (Text-figs. 6 D and F)

From the pale brown ovotestis, the greatly convoluted white hermaphrodite duct enters the albumen gland, with the usual "claw" or seminal vesicle. The common duct is voluminous and folded, the male or prostatic portion yellow and the female part pinkish-grey. The first part of the free oviduct is short and slender, and the longer distal part dilated. This part contains two prominent longitudinal folds of mucous membrane forming the ligula as in *A. hortensis*. The spermatheca duct is bulbous at its origin, then longer and more slender than in *A. hortensis*, and ends in a larger spherical spermatheca sac. The vas deferens and epiphallus are very similar to those of *A. hortensis*, but the terminal annular thickening is more pronounced. The upper atrium is small, the yellow glandular lower atrium of medium size with a wrinkled mucous membrane.

*Spermatophore* (Text-fig. 6 G)

Very different from that of *A. hortensis*: about 20 mm long, slender anteriorly, then dilating, to taper again to an almost filamentous tail. The convex edge is finely denticulate.

*Mating*

Mating occurs in March, April and May, and perhaps other months. One of a pair follows the other for about half an hour, "licking" the caudal mucus. Then they curve around in a semicircle with the right side of the necks in contact. In about fifteen minutes the lower atria are everted as small yellow eminences. These rapidly enlarge as eversion is completed, and the combined atria form an ovoid bluish-white mass between the two animals, the junction of the two atria being barely visible as a fine line. After three-quarters of an hour the mass shrinks and the animals separate, and the spermatophores are momentarily visible, partly protruding from the spermatheca ducts as the remainder of the shrinking mass is withdrawn. For further details see Quick (1946). The slender portion of the free oviduct is not everted as a stimulator as it is in *A. hortensis*, where this portion of the oviduct is longer. The combined mass resembles that of *A. ater*, since the differing situation of the ligula does not affect the aspect.

### *Development*

The opaque leathery eggs, measuring from  $2.25 \times 2.25$  to  $3.25 \times 2.25$  mm, vary considerably in size and shape, even in the same cluster. Eggs are laid three weeks after mating. They are laid in masses of up to fifty, and tend to adhere together, several eggs sometimes being enclosed in a common tubular coat of mucus. They are white at first and become yellow or brown. Hatching occurs in from three to five weeks. The newly hatched young are about 6 mm long, grey, with darker dorsal region, and with lateral body and mantle bands. The tentacles are violet. Newly hatched *A. ater* are orange, straw colour or pale greenish-grey, and the tentacles dark grey rather than violet; but the most notable difference is that the anterior ends of the mantle bands are closer together than in *A. subfuscus* (Pl. I, figs. 9 and 11).

### *Ecology*

*A. subfuscus* lives under logs and litter in deciduous and coniferous woods, and is one of the few species found in pine woods. It is also frequent in damp hedgerows, waste ground and some gardens. It feeds on the algal and fungal film on logs, and also on the larger fungi. In captivity it readily eats carrot, lettuce, oatmeal and dead slugs (Map 8).

### *Distribution*

The whole of Great Britain and Ireland, except possibly parts of East Anglia and eastern Scotland. Most of Europe, north of a line through Orenburg and Odessa (Russia), northern Italy, Barcelona and Oporto. Introduced into North America.

### *Material examined*

Living from many places in Britain. Spirit material from Britain, France, Luxembourg, Germany, Italy and Madeira.

### *Arion lusitanicus* Mabille, 1868

*Arion lusitanicus* Mabille, 1868 : 134. La Sierra d'Arriba, near Lisbon.

### *Notes*

The name *lusitanicus* is applied to this species with some hesitation, since Mabille (1868) described the tubercles as "peu allongés". However, Pollonera's description and figures (1889 : 626, pl. 9) leave little doubt about the identification. *A. nobrei* Pollonera (1889) is similar to *A. lusitanicus* but smaller, with smaller tubercles, completely black, and with the distal genital ducts even more strongly pigmented. A specimen from Portugal in the B.M. (N.H.) collections, identified as *A. nobrei*, agrees with this description.

Cain & Williamson (1958) discuss specimens of *Arion* collected at Nuneaton, Warwickshire, which perhaps suggest that the status of *A. lusitanicus* in Britain may require further investigation.

*First British record*

By Collinge (1893). Though again recorded by Collinge (1897*a*), the species was overlooked by Taylor (1902-07) and by other authors on the British fauna (e.g. Roebuck, 1921; Kennard & Woodward, 1926; Ellis, 1926 and 1951; Quick, 1949), until its rediscovery in Durham by Mrs. Vincent (Quick, 1952).

*Diagnostic features*

Large, up to 10 cm in length, with coarse tubercles like *A. ater*; from which it is internally distinguished by the dilated distal part of the free oviduct, which lodges the ligula. Distinguished from *A. subfuscus* by coarse tubercles and a longer spermatheca duct.

*External appearance*

The length when crawling is from 7 to 10 cm. The colour varies as in *A. ater*, and may be dark grey, reddish-yellow, brown or dull greenish-grey, with darker head and tentacles. The transversely lineated foot fringe is sometimes darker and sometimes lighter than the body, and the sole is generally pale, but dark in some Nuneaton specimens. The respiratory orifice does not dilate to the same extreme degree as in *A. ater*. In the younger stages there is on each side a dark lateral band (Text-fig. 5 D). On the mantle the bands form a lyre-shaped figure, the right band surrounding the pulmonary orifice on all sides, and anteriorly they are a little closer together than in *A. subfuscus* of similar size. Sometimes the bands are retained up to maturity.

*External variation*

Var. *rufescens* Collinge (1893), body dark red, sides of body bandless; var. *nigrescens* Collinge, black or plumbaceous; var. *olivaceus* Collinge, various shades of olive-green; var. *flavogriseus* Collinge, yellowish-grey, foot fringe lighter than the body.

*Pallial organs, retractor muscles, nervous system*

As in *A. ater*.

*Jaw*

Intermediate in size (3 mm across) between those of *A. subfuscus* and *A. ater*; arcuate, crossed by from nine to thirteen rather broad even ribs; pale brown or yellow in light examples, nearly black in dark ones.

*Radula* (Text-fig. 3 G)

Intermediate in size between those of *A. subfuscus* and *A. ater*. The formula varies (in adult specimens from Durham) between C.17.35 and C.19.45.

*Alimentary system*

As in *A. ater*.



*Reproductive system* (Text-figs. 5 A and E)

The very dark ovotestis lies a little further forward than in *A. ater*. The dilated central part of the hermaphrodite duct is folded in a zig-zag manner, and then narrows to form the usual "claw" at the albumen gland, which varies in size with the maturity of the animal. A yellowish-pink fold or ruffle accompanies the first part of the sperm-oviduct. The free oviduct is slender at first, and then becomes greatly enlarged, to narrow again slightly where it enters the upper atrium. This dilated part, in both the Durham and the Nuneaton examples, is deeply pigmented in a characteristic way (Text-fig. 5 A). The spermatheca duct is rather longer than in *A. subfuscus*, somewhat dilated at the origin. It also sometimes shows a slight dilatation, with stronger mucous folds, between the origin and the spherical spermatheca sac. The vas deferens is about as long as the epiphallus, and the latter shows a conspicuous annular ring at its termination. The distal half of the epiphallus is deeply pigmented like the oviduct, the pigment usually tailing off in two tongues. In some individuals this pigmentation is less pronounced. The upper atrium is small, the lower pear-shaped with thick glandular-looking walls, sometimes yellow, and sometimes sprinkled with minute spherical white granules.

The upper atrium contains no ligula, but the distal dilated part of the oviduct contains two conspicuous folds which apparently represent this structure, and function similarly (Text-fig. 5 E). In *A. ater* the ligula occupies the large upper atrium in both young and adult animals. Examination of the genital ducts of immature animals of *A. subfuscus* and *A. lusitanicus* (Text-figs. 6 C and D) shows that the ligula lies in the oviduct, as in the adult, and does not "migrate" upwards or downwards. It is noteworthy that in young *A. ater* the oviducal branch of the genital retractor is inserted as in *A. hortensis*, *A. subfuscus* and *A. lusitanicus*; while in adult *A. ater* (Text-fig. 6 K) the distal part of the oviduct becomes relatively much shorter, bringing the retractor close to the atrium. It could be argued that the lateral atrial pouch of *A. ater* is homologous with the dilated terminal portion of the oviduct of the other species, or alternatively that this portion of the oviduct is a diverticulum of the atrium. Seeing that this portion is so well developed in the early stages of growth, the second alternative is unlikely. There is in *Geomalacus maculosus* a long backward extension of the atrium; but this carries back the epiphallus and the spermatheca, and does not affect the oviduct.

*Spermatophore* (Text-figs. 6 H and I)

A chitinous tube 20 mm long, armed with a spiral row of serrations, most prominent towards the anterior end; and two low smooth ridges at the posterior end, which die out anteriorly.

*Mating* (Text-fig. 6 E)

The figure shows the appearance of the reproductive organs just before they are withdrawn after mating, with the partner's spermatophore protruding from the spermatheca duct. Observations on the mating of *A. lusitanicus* are too few and incomplete to permit of comparison with the other species.

*Development*

The white eggs measure about  $3 \times 3.25$  mm, but vary considerably in size and shape, both within and between clusters, and become yellower with age. In the laboratory, they have been laid in January and in March; and in September by laboratory-bred animals only five or six months old. The clusters contain up to about fifty eggs, bound together by mucus, which hatch in about three weeks in the laboratory.

*Ecology*

In captivity, like most other slugs, *A. lusitanicus* is readily reared on lettuce, cabbage, oatmeal, etc.; but little is known of its habits in the wild.

*Distribution* (Map 9)

In the British Isles, known only from Berehaven, Bantry Bay, Ireland (Collinge, 1893); the garden of No. 24, North Bailey Road, Durham and the river bank adjoining (Quick, 1952); and the site of bombed cottages at Attleborough, Nuneaton, Warwickshire (Cain & Williamson, 1958). On the Continent, known from near Lisbon, Portugal; Mentone and Pyrenées Orientales, France; and Basle, Switzerland. The species may be indigenous to Ireland and but recently introduced to Durham and Nuneaton, though it seems firmly established there. Probably it is more widely distributed in Britain, but has not been distinguished from *A. ater*.

*Material examined*

Living specimens from Durham and Nuneaton. Spirit specimens from Basle, Switzerland, and the Pyrenées Orientales. An immature specimen from Bantry Bay (Collinge Collection, Museum of Zoology, Cambridge) probably belongs to this species.

*Arion ater ater* (Linnaeus, 1758)

*Limax ater* Linnaeus, 1758 : 652. Sweden.

*Arion empiricorum* Férussac, 1819 : 60, pls. 1-3 (in part).

*First British record*

By Lister (1674).

*Diagnostic features*

Large size, coarse tubercles, wide foot fringe, large respiratory orifice; short free oviduct surrounded by genital retractor muscle, ligula in upper atrium. Adults not certainly distinguishable in outward appearance from *A. a. rufus*, but usually black or dark brown with a grey sole, and rarely with a brightly-coloured foot fringe. Lateral pouch and ligula much smaller than in *A. a. rufus*, and vas deferens usually shorter. Upper atrium shorter than lower atrium.

*External appearance* (Pl. 1, fig. 3)

Length when fully extended generally about 14 cm, but may be even longer. The body tubercles are long and prominent, and darker than the furrows except in the young. The mantle is shagreened. There is no trace of a dorsal keel at any stage. The caudal mucus pore is conspicuous. The sole is more or less divided into median and lateral areas, the lateral areas usually the darker. The wide foot fringe is transversely lineolated, and in dark specimens the lines extend into the lateral areas of the sole. In pale individuals (except true albinos, which are rare) the head and tentacles are much darker than the rest of the body. The respiratory orifice is absolutely and relatively larger than in the previously described species. The very sticky body mucus may be colourless, or yellowish in red and yellow forms, that from the caudal pore always colourless. At rest, *A. ater*, like *A. lusitanicus*, but unlike *A. subfuscus* and the smaller species, can contract to a hemispherical shape, or even a larger portion of a sphere.

*External variation*

Since *A. a. rufus* has been generally considered as only a variety of *A. ater*, it is impossible at present to tell which of the very numerous named varieties belong properly to the latter. Probably most of the brighter varieties belong to *A. a. rufus*, and of the duller ones to *A. a. ater*.

Extensive lists of varieties are given by Taylor (1902-07), Kennard & Woodward (1926) and Hesse (1926), of which the following is a short selection: var. *ater* Linnaeus (1758), black with grey sole; var. *aterrima* Taylor (1905), completely black; var. *alba* Linnaeus (1758), white; var. *albida* Roebuck (1883), white with yellow fringe; var. *castanea* Dumont & Mortillet (1856), brown with paler fringe; var. *albolateralis* Roebuck (1883) (? = var. *media* Jensen, 1873), dorsum black, sides white; var. *reticulata* Roebuck (1885), tubercles pale, furrows pigmented (i.e. the juvenile colouring retained by the adult); var. *hiberna* Mabille (1868), rusty purple with paler sides; var. *plumbea* Roebuck (1884a), leaden grey with yellow fringe; var. *succinea* Müller (1774), yellow with red or orange fringe; var. *coccinea* Gistel (1848), vermilion; var. *marginella* Schrank (1803), black with red fringe.

*Pallial organs*

Large vessels occupy the roof and floor of the pulmonary chamber. The kidney is curved into a rounded quadrangular form, surrounding the pericardium, and the ventricle lies posteriorly to the auricle. The anterior branch of the aorta curves round the anterior loop of the intestine, then runs forwards supplying branches to the anterior part of the body, passing between the visceral and pedal ganglia. The posterior aorta runs backwards and supplies the alimentary and genital systems, and passes between the visceral and pedal ganglia. The ureter and rectum terminate at the posterior lip of the respiratory orifice.

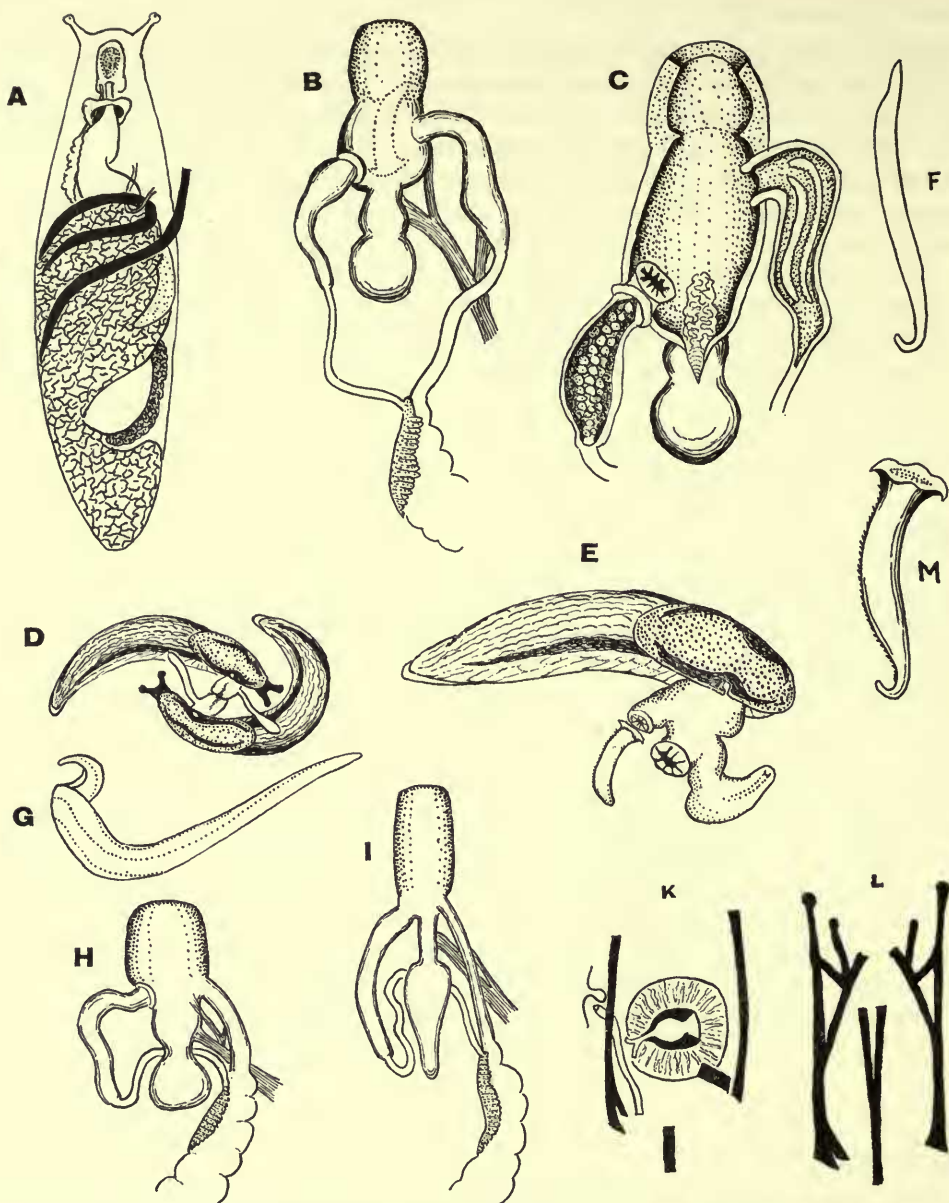


FIG. 4. *Arion*. A. *A. hortensis*—internal organs *in situ* ( $\times 2$ ) showing liver, exposed part of stomach, part of ovotestis, albumen gland, intestine, aorta, crop, left salivary gland, nerve ring, characteristic pigmented area on buccal bulb. B. *A. hortensis*—distal genital ducts ( $\times 4$ ) with position of the partner's spermatophore indicated on upper atrium. C. *A. hortensis*—distal portion of genital ducts ( $\times 5.3$ ) opened to show ligula in oviduct, glandular area below spermatheca, and papillate mucous membrane of epiphallus. D. *A. hortensis*—mating pair ( $\times 1.3$ ) with slender parts of oviducts everted and functioning as stimulators. E. *A. hortensis*—individual



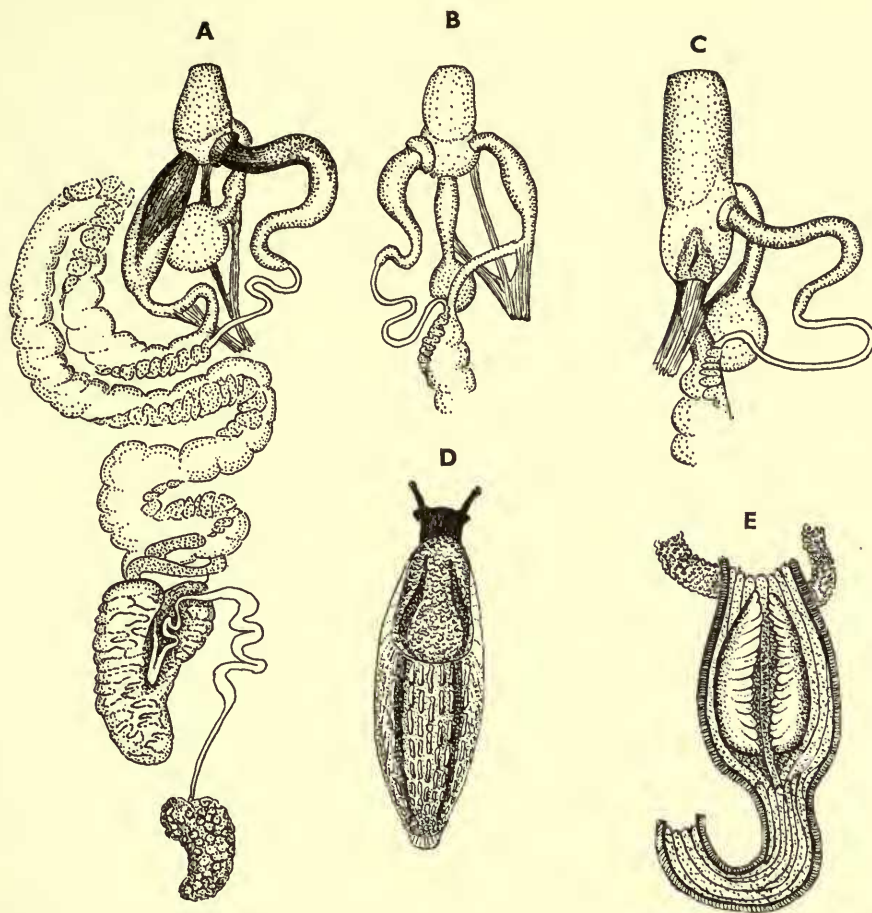


FIG. 5. *Arion*. A. *A. lusitanicus*—reproductive organs ( $\times 3$ ). B. *A. subfuscus*—distal genital ducts ( $\times 3$ ). C. *A. ater ater*—distal genital ducts ( $\times 3$ ). D. *A. lusitanicus*—young individual ( $\times 10$ ). Compare mantle bands with those of young *A. subfuscus* and *A. ater* (pl. 1, figs. 9 & 11). E. *A. lusitanicus*—oviduct ( $\times 5.3$ ) opened to show position of ligula.

immediately after coitus ( $\times 2$ ) with everted genitalia, showing atria, everted oviduct, papillate epiphallus, partner's spermatophore adhering to base of spermatheca duct. F. *A. hortensis*—spermatophore ( $\times 6.7$ ). G. *A. fasciatus*—spermatophore ( $\times 4$ ), adapted from Lohmander. H. *A. intermedius*—distal genital ducts ( $\times 4.7$ ). I. *A. fasciatus*—distal genital ducts ( $\times 4$ ). K. *A. hortensis*—pallial region in ventral view, showing kidney, pericardium, auricle, ventricle, rectum and respiratory orifice. Muscles cut short. L. *A. hortensis*—cephalic and buccal retractor muscles, ventral view. M. *A. ? hortensis*—spermatophore ( $\times 6.7$ ) of a slug from a garden in Eaton Crescent, Swansea, Glamorgan.



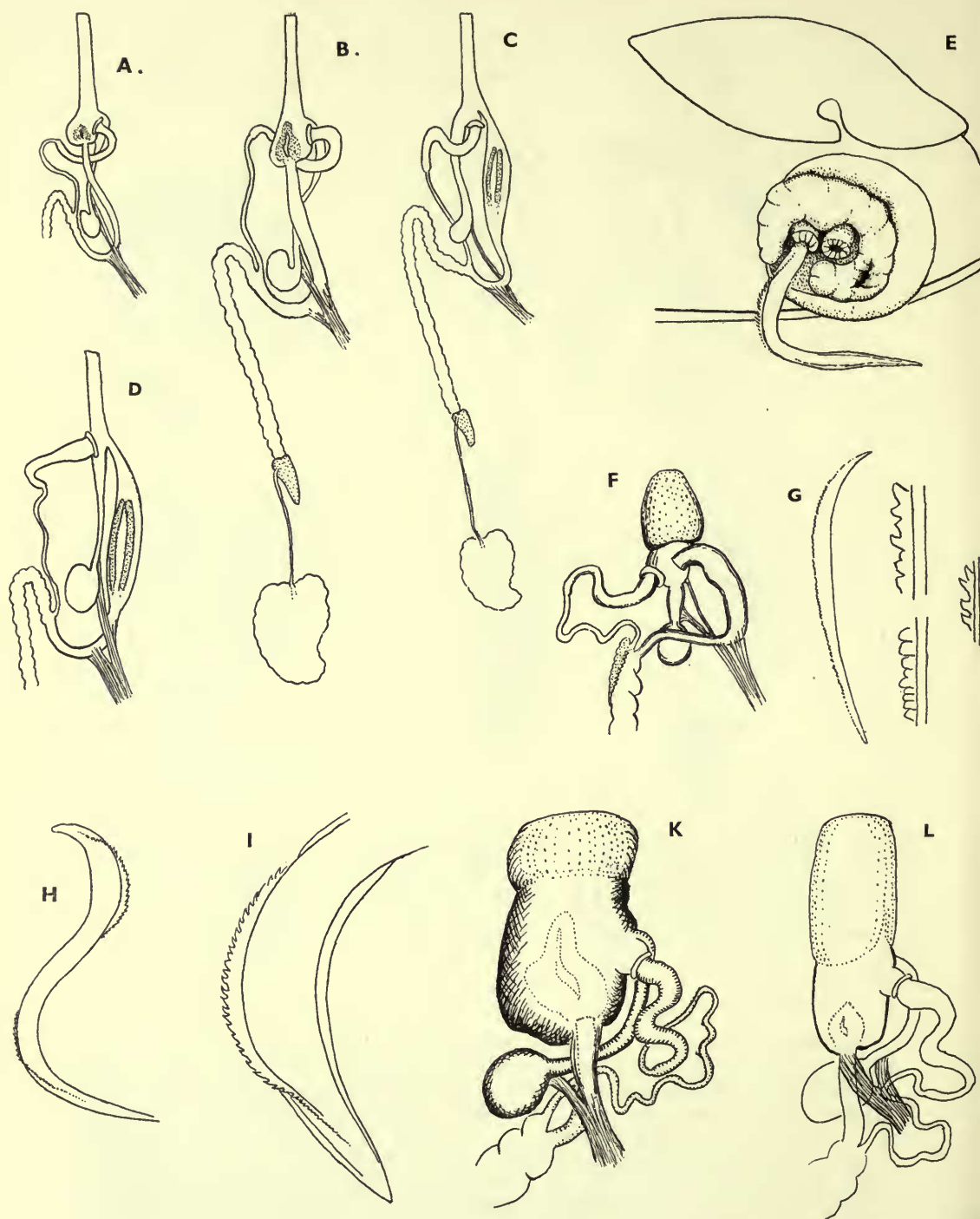


FIG. 6.

*Retractor muscles*

The right and left cephalic retractors are widely separated at their origin, from the diaphragm behind the kidney. The pharyngeal retractor arises from the median dorsal body-wall. The genital retractor arises from the diaphragm immediately in front of the origin of the left cephalic retractor, ensheathes the short free oviduct, and sends a branch to the spermatheca duct.

*Nervous system* (see Text-fig. 7 M)

Highly concentrated in the adult, the commissures being short and the visceral ganglia closely united.

*Jaw*

Strong, arcuate, 3.5 mm across, crossed by a varying number of ribs (up to eighteen), variable in breadth, which denticulate the upper and lower edges. Colour yellow in pale specimens, nearly black in dark ones, the attached margin being darker than the free cutting edge.

*Radula* (Text-fig. 3 F)

7–8 mm long by 3 mm wide. The number of lateral teeth varies from 20 to 25, and of marginals from 40 to 46 on each side, but the average formula is  $C.22.44 \times 130$ .

*Alimentary system*

The short oesophagus leads through a large wide crop to the stomach, which forms the posterior part of the alimentary canal. The salivary glands on each side of the crop are large, flattened and much lobulated. The intestine, with one anterior loop, is twisted through about one and a half turns—more than in the young of the smaller species.

*Reproductive system* (Text-figs. 5 C and 6 I.)

The proximal parts resemble those of other species of *Arion* (see Text-fig. 5 A).

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FIG. 6. *Arion*. A. *A. ater ater*—distal genital ducts ( $\times 10$ ) of a young individual, showing long atrium and position of ligula. B. *A. ater ater*—genital organs ( $\times 3.3$ ) of a nearly full-grown but immature individual, showing relative sizes of ovotestis, albumen gland, common duct and distal portions of ducts. C. *A. lusitanicus*—genital organs ( $\times 6.7$ ) of an immature individual, showing relative sizes of organs and position of ligula. D. *A. subfuscus*—distal genital ducts ( $\times 6.7$ ) of a young individual, showing ligula in lower oviduct. E. *A. lusitanicus*—slug after coitus, with atrium everted. The ligula, with the oviducal orifice in its lower anterior part, surrounds the orifices of epiphallus and spermatheca. The partner's spermatophore projects from the spermatheca duct. F. *A. subfuscus*—distal genital ducts ( $\times 3.3$ ). G. *A. subfuscus*—spermatophore ( $\times 3.3$ ), and portions of spermatophore ( $\times 16.7$ ) from near anterior end, centre and posterior end. H. *A. lusitanicus*—spermatophore ( $\times 3.5$ ). I. *A. lusitanicus*—portion of posterior end of spermatophore ( $\times 11$ ). K. *A. ater rufus*—distal genital ducts ( $\times 3.3$ ). L. *A. ater ater*—distal genital ducts ( $\times 3.3$ ).

The short free oviduct, ensheathed by the genital retractor, enters the upper atrium apically. It is not dilated, and does not contain the two conspicuous folds of *A. hortensis*, *A. subfuscus* and *A. lusitanicus*. However, the upper atrium contains a somewhat similar folded mass, arising from the walls of the atrium and the termination of the oviduct, known as the ligula. This is much smaller than in *A. a. rufus*, where it is contained in a lateral enlargement of the atrium. The spermatheca duct is relatively longer than in *A. intermedius*, *A. fasciatus*, *A. hortensis* and *A. subfuscus*, is not bulbous at the base, and receives a branch from the genital retractor. The vas deferens is usually less than one and a half times as long as the epiphallus, which terminates in a thickened ring at the atrium.

#### *Spermatophore* (see Text-fig. 7 L)

This rapidly disintegrates in the spermatheca, so that it can only be obtained intact soon after coitus. Two specimens were obtained in this way, which are 17 and 18 mm long. Each is somewhat dilated near the proximal end, and tapers in each direction. A finely serrated ridge runs nearly the whole length, the serrations pointing forwards. The epiphallus measures only 11 mm long in alcohol specimens; so, unless it is much longer in life, part of the spermatophore must be formed during coitus.

#### *Mating*

Occurs in June and July, at any rate in Wales, after dark. After about half an hour of following and licking, the animals curve in a semicircle, neck to neck, and evert their atria to form a bluish-white mass. They separate after about half or three-quarters of an hour, when the spermatophores can be seen protruding from the spermatheca ducts, while the shrinking ligulae and atria are quickly withdrawn. Adams (1910), Gerhardt (1940) and Quick (1947) give fuller details.

#### *Development*

The eggs are variable in size, usually about  $5 \times 4$  mm. They are opaque and leathery, pearly white when laid but turning brown. They are laid in clusters in the soil, two or three weeks after coitus. The first cluster may contain 150 eggs or more, and one or two subsequent clusters fewer than this. The eggs hatch in from four to six weeks. The young, 10 mm long, are pale straw colour or sometimes greenish, with darker head or tentacles. They are usually bandless, and if faint bands appear after a few days they quickly fade. Yellow pigment is concentrated in the tubercles. In the young of dark varieties the black pigmentation begins in the dorsal furrows and spreads downwards, producing a reticulate pattern which very occasionally persists in the adult; though as a rule the pigment of pale adults is concentrated in the tubercles, leaving the furrows paler. The sole is the last part to pigment.

Like the other species of *Arion*, *A. ater* shows in the later stages of embryonic development a cephalic and a caudal vesicle, which pulsate alternately. The tubular caudal vesicle persists to within a few days of hatching (Text-fig. 18 F). The jaw at hatching does not show any sign of bilateral origin like that of *Agriolimax*.

*Behaviour*

Adults of *A. ater* exhibit a peculiar rolling reflex, if touched when fully (or almost fully) contracted. The body sways from side to side with a simultaneous screwing motion, with a periodicity of about two seconds. The movement cannot always be elicited, but may be quite violent. As far as is known, no other slugs show this reflex. It is tempting to explain it in terms of alternate contraction of the cephalic retractors, which have separated origins in *Arion*. However, the reflex is only doubtfully elicited from *A. lusitanicus*, and repeated attempts to elicit it from other British species of *Arion* have always failed.

*Ecology*

*A. a. ater* is practically omnivorous, eating decayed vegetable matter, dead mice and rabbits, and animal faeces. In the lowlands, it is common in grass fields, woods, hedgerows and waste ground, and on grassy downs and sea cliffs. It is often the only mollusc present on upland peaty moors and sphagnum bogs, where it is smaller than in the lowlands, and either black (often the var. *aterrima*) or very dark brown.

*Distribution* (Map 10)

The whole of the British Isles, northern and central Europe, Iceland and ? Russia. Probably some of the records from Spain, Portugal, Italy and the Mediterranean coasts and Atlantic isles refer to the related forms (*A. a. rufus*, *A. lusitanicus* and possibly others). Introduced into North America.

*Material examined*

Living specimens of *A. a. ater*, as distinct from *A. a. rufus*, have been identified from the following localities in the British Isles: Exeter, Littlehampton and Collompton in Devon; Netley Heath, Surrey; Howe Wood near Littlebury, Essex; Reading, Berkshire; Thorpe St. Andrews, Brundall Marshes and Wheatfen Broad in Norfolk; Little Shelford, Homingsea and Durnford Fen in Cambridgeshire; Cefn Bryn, Gower and Llangennith in Glamorgan; Capel-y-ffin, Brecon; Skokholm Island, Pembroke; Abersoch, Caernarvon; Bromborough, Cheshire; Pentland Hills, Edinburgh; Courtmacsherry, Cork.

*Arion ater rufus* (Linnaeus, 1758)

*Limax rufus* Linnaeus, 1758: 65. ? Sweden.

*Arion empiricorum* Férussac, 1819: 60 (in part).

*Arion sulcatus* Morelet, 1845: 28.

*Notes*

See Quick (1947). Økland (1923) believes it to have been introduced to Sweden in historical times. Férussac's *empiricorum* includes *A. a. ater*, *A. a. rufus*, and perhaps also *A. lusitanicus* and other species. Moquin-Tandon's description (1855-56, 2: 10) of *empiricorum*, and his fig. 1 on pl. 1, could serve for either *A. a. ater* or



*A. a. rufus* ; but his fig. 12 represents the genitalia of *A. subfuscus*, *A. lusitanicus* or a similar species.

Cain & Williamson (1958) have studied pigmentation and genital anatomy in populations referable to *A. a. ater* and *A. a. rufus*. Their evidence suggests that only the former is indigenous to the British Isles, where *A. a. rufus* is an introduced alien associated with cultivated land. In Europe the natural ranges of the two forms seem not to overlap widely, since *A. a. ater* apparently occupies Scandinavia and *A. a. rufus* much of the rest of the continent, but it is not yet known how the two forms interact along their natural boundary. However, two populations near Oxford show the intermediacy of character combined with high variability which is to be expected from hybrids. This suggests that the two forms should be considered as geographical races.

#### *First British record*

By Gerhardt (1940), on specimens from Swansea, Glamorgan. The subspecies had been considered by previous British authors as merely a variety of *A. a. ater*.

#### *Diagnostic features*

Adult not certainly distinguishable from *A. a. ater* on external appearance, but usually yellow to reddish-brown, with a creamy yellow sole and bright orange or red foot fringe. Internally, upper atrium longer than lower, much larger ligula in lateral pouch, vas deferens usually longer than in *A. a. ater*. Young have mantle bands, rarely found in *A. a. ater*.

*External appearance, external variation, pallial organs, retractor muscles, nervous system, jaw, radula, alimentary system*

As in *A. a. ater*.

#### *Reproductive system* (Text-fig. 6 K)

As in *A. a. ater*, except for the distal genital ducts. The upper atrium is larger, and exhibits a lateral bulging that lodges a much larger ligula. The lower atrium is shorter than the upper. The vas deferens is relatively longer, usually more than one and a half times as long as the epiphallus and sometimes nearly twice as long. The oviduct, instead of entering the apex of the atrium formed by the lateral bulge, enters between this and the entrance of the epiphallus. Sometimes (as in specimens from Limeslade Bay, Swansea) the lateral bulge is narrower and prolonged further backwards. Occasional specimens of *A. a. ater* show a suggestion of a lateral bulge, but the size of the ligula, and the relative sizes of upper and lower atria and the vas deferens and epiphallus, serve to identify it.

#### *Spermatophore* (Text-fig. 7 L)

Probably longer than that of *A. a. ater* (about 25 mm long), and even more disproportionate to the size of the epiphallus in spirit material. This may be associated with the longer period of coitus, if the spermatophore is formed during coitus.



### *Mating*

*A. a. rufus* attains maturity later in the year than *A. a. ater*, and mates in September and October, at any rate in South Wales. Mating resembles that of *A. a. ater*, except that coitus lasts for two hours. For further details, see Gerhardt (1940) and Quick (1947).

### *Development*

The eggs are like those of *A. a. ater*. The newly-hatched young are pale yellow or orange, and differ from those of *A. a. ater* in having (at birth or after a few days) dark mantle and body bands, which persist for a few months. In individuals which will be dark when adult, the course of pigmentation is as in *A. a. ater*. The young can be distinguished from those of *A. subfuscus* by their coarser tubercles, and by the closer approximation anteriorly of their mantle bands (Pl. 1, figs. 9 and 11).

### *Behaviour*

*A. a. rufus* shows the same rolling reflex as *A. a. ater*.

### *Ecology*

In Britain, *A. a. rufus* is more likely to be found in gardens and parks (though sometimes at a considerable distance from dwellings) than in wilder places. It never seems to occur in peaty moors or sphagnum bogs; though this may reflect its introduction by man, and consequent restriction to cultivated land, rather than dependence on calcium in the soil.

### *Distribution* (Map 11)

Not fully known, since *A. a. rufus* has only recently been distinguished sub-specifically from *A. ater*. Authentically known in Britain from Glamorgan, Somerset, Berkshire, Oxford, Essex, Cambridge and Leicestershire. It seems to be the native form in Europe south of Denmark, though the natural ranges of the two subspecies are insufficiently known.

### *Material examined*

Living specimens from Monkton Coombe near Bath, Somerset; Chingford, Essex; Basildon, Berks; Coombe End, Oxford; Lords Meadow near Cambridge; and the Swansea district, Glamorgan. Spirit material from Loughborough, Leicestershire; Borgholm, Öland Island, Sweden; Froedensborg, NE. Zealand, Denmark; Canton Solothurn, Switzerland; and from France, Corsica and Portugal.

## Superfamily ZONITACEA

### Family LIMACIDAE

Slugs with a small calcareous shell almost always completely enclosed by the mantle. The dorsum is keeled posteriorly or right up to the mantle. There is no

caudal mucus gland. The sole is tripartite and a supra-pedal groove is present (aulocopod). The jaw is smooth, usually with a median projection (oxygnath), and the lateral radular teeth are tri- or bicuspid, the marginal teeth aculeate. The spermatheca duct is short, generally arising from the atrium.

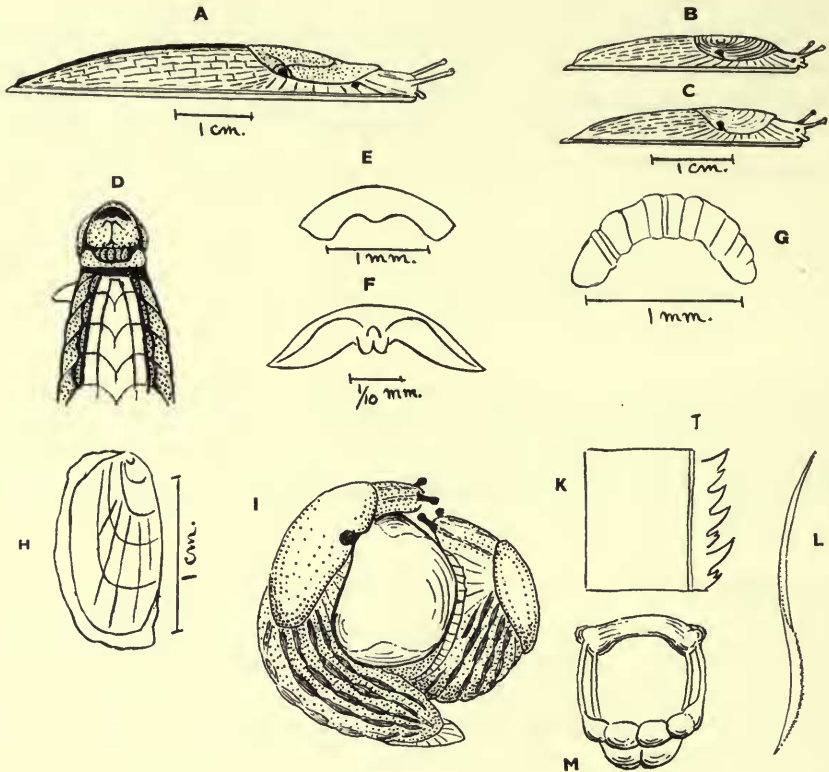


FIG. 7. Limacidae. External appearance. A. *Milax*—keel extending forward to mantle; mantle granulate with horseshoe furrow; respiratory orifice behind centre of mantle; genital orifice between upper tentacle and respiratory orifice. B. *Agriolimax*—keel extending only a little way forward; tail truncate; mantle concentrically ridged with nucleus over respiratory orifice, behind centre of mantle; genital orifice close behind upper tentacle. C. *Limax*—keel extending a little way forward; tail not truncate; mantle concentrically ridged with nucleus in median dorsal line; respiratory orifice behind centre of mantle; genital orifice close behind upper tentacle. D. *Milax*—chevroned foot-sole, stimulator protruded.

E. *Lehmannia marginata*—jaw. F. *Agriolimax reticulatus*—jaw of very young individual, showing bilateral origin. G. *Arion hortensis*—jaw, for comparison. H. *Limax maximus*—shell.

*Arion ater rufus*. I. Pair in copula. K. Portion of posterior end of spermatophore ( $\times 24$ ). L. Spermatophore ( $\times 1.7$ ). M. Ganglia and commissures of nerve ring (buccal ganglia omitted).

## Subfamily PARMACELLINAE

The shell is paucispiral, not completely enclosed by the mantle (in *Parmacella*), or flat and enclosed (in *Milax*). The mantle is granular, bearing a horseshoe-shaped groove, and the respiratory orifice lies behind the middle of the right margin. The genital orifice is between the respiratory orifice and right upper tentacles. The dorsum is keeled up to the mantle. The central and lateral radular teeth are tricuspid. The intestine has one forwardly directed loop, and the rectum lacks diverticula. An epiphallus secretes a spermatophore, and atrial glands are present. *Milax* is the only British genus.

Watson (1930) considers that *Parmacella* and *Milax* arose from a common stock ; *Parmacella*, with its spiral shell, embedded pedal gland, and ocular retractor crossing the penis, being the more primitive.

Genus *MILAX* Gray, 1855

Type species *Limax gagates* Draparnaud, 1801.

The shell, completely enclosed by the mantle, has a median non-spiral nucleus near the posterior margin. The pedal mucus gland lies free in the body cavity, and not embedded in the foot below it, as in the other genera. The right ocular retractor lies to the left of both penis and vagina. In *M. sowerbyi* and *M. gagates* an atrial stimulator is present. The median area of the sole is crossed by  $\Lambda$ -shaped grooves. *Milax* is without lateral body bands at all stages of growth.

Watson (1930) considers that, of the British species of *Milax*, *M. gagates* (with more lateral and fewer marginal radular teeth, and a wider distribution) is the most primitive, and *M. budapestensis* (with fewer lateral and more marginal teeth, and no stimulator) the most specialized.

A common continental species, *M. marginatus* (Draparnaud, 1801) (= *M. rusticus* Millet, 1843), which it seems possible may yet be discovered in Britain, is a yellowish slug with small black spots on the body and mantle and a dark band on each side of the latter, and resembles *M. budapestensis* in lacking the atrial stimulator.

*Milax gagates* (Draparnaud, 1801)

*Limax gagates* Draparnaud, 1801 : 100. Presumably near Montpellier, France.

*Amalia parryi* Collinge, 1895a : 7.

*Amalia babori* Collinge, 1897c : 294.

## Notes

Two species are currently confused under the name *gagates*. The common British species is distinguished by its smooth genital stimulator, and less certainly by its smoother appearance (with flattened tubercles) and paler sole. The second species is primarily Mediterranean in distribution, though there is one hitherto unpublished

British record (p. 156). It has two rows of large papillae on the stimulator, and also more prominent tubercles and a darker sole.

It is not easy to determine the proper application of the name *gagates*. There are no slugs among Draparnaud's types at the Naturhistorisches Museum, Vienna (Locard, 1895 : 154 ; confirmed by Dr. O. E. Paget *in litt.*). Both species occur at Marseilles, only eighty miles from Draparnaud's home at Montpellier. Draparnaud's description does not deal with the internal anatomy. However, he describes *gagates* as " très-lisse, très-luisante " (1801) and " nitidus ; corpore striato subrugoso " (1805). This strongly suggests the north-western species, since he applies " subrugosus " to other slugs as smooth as this, and uses " rugosus " only for those as rough as the Mediterranean species.

Few early authors described or figured the condition of the stimulator, from which alone their application of the name *gagates* could be determined. Lessona & Pollonera (1884 : 105, pl. 2, fig. 2) use this name for Italian slugs with papillate stimulators. Germain (1930, fig. 52 A), in treating the French fauna, gives a figure of a papillate stimulator which is apparently copied from Lessona & Pollonera, and does not mention the locality. Taylor (1902-07, fig. 159) shows the smooth stimulator of a British slug.

The name *parryi* Collinge is a synonym of *gagates*, as the latter is here interpreted, since one of the type specimens from Santa Cruz, Teneriffe, shows on dissection a penis, epiphallus and stimulator like the British species. So does one of a series from Haleakala Maui, Hawaii, apparently the types of *babori* Collinge. The following names, among others, cannot at present be allocated to either of the species with any certainty :

*Limax maurus* Quoy & Gaimard, 1824 : 427. Port Jackson, Sydney, Australia.

*Parmacella nigricans* Schultz, 1836, 1 : 125. Palermo, Sicily.

*Amalia mediterranea* Cockerell, 1891 : 331. Algeria.

*Amalia mediterranea* forma *similis* Cockerell, 1891 : 332. Catania, Sicily.

However, specimens that I received from Catania in 1947 proved to be the species with a papillate stimulator.

#### *First British record*

By Thompson (1840 : 205).

#### *Diagnostic features*

Uniform grey or black colour, with darker keel, respiratory orifice without pale margin, mucus colourless ; smooth genital stimulator, rather thick spermatophore, not hooked at the thick end and with spines distributed more evenly than in *M. sowerbyi*.

Differs from *M. cf. insularis* in smooth, not papillate, stimulator ; and less certainly in smoother skin and paler sole.

#### *External appearance* (Pl. I, fig. 12)

Length extended about 5 cm. When contracted, the slug is more compressed laterally than *M. sowerbyi*. The colour is usually grey or black, getting lighter



towards the foot. The tubercles are flattened, making the slug rather smooth, and the intervening grooves are unpigmented. The keel is usually dark, and is abruptly angulated at the posterior end. The central area of the granulate mantle is delimited by a horseshoe-shaped groove, open posteriorly, with the arms angulated at the level of the respiratory orifice. The respiratory orifice is small and without a pale border, and is situated a little behind the centre of the right margin of the mantle. The sole is pale, distinctly tripartite, with the median zone crossed by  $\Lambda$ -shaped grooves (Text-fig. 7 D). Only this central area shows the locomotory waves. The mucus is sticky and colourless.

### *External variation*

Var. *plumbea* Moquin-Tandon (1855), paler or darker grey; var. *rava* Williams (1888), drab coloured, slightly fuscous, mantle paler; var. *bicolor* Taylor (1904), deep red on the sides; var. *benoiti* Lessona & Pollonera (1882), black, keel whitish.

Other varieties with a Mediterranean distribution mentioned by Taylor (1902-07: 143-146) probably refer to *M. cf. insularis*.

### *Shell* (Text-fig. 8 K)

Measures about  $4 \times 2.5$  mm. White and shining. Somewhat saddle-shaped above, and flattened below. The nucleus is near the posterior margin, in the middle line, and the lines of growth are distinct. Viewed laterally, the shell is concave from back to front, with the nucleus at the highest point, and shows a groove separating the upper part of the shell from the lower.

### *Pallial organs*

The kidney has an extension to the right toward the rectum, and the auricle and ventricle lie anterior to the left half of the kidney. The rectum crosses over the common origin of the tentacular and pharyngeal muscles to the posterior lip of the respiratory orifice.

### *Pedal gland*

Lies free in the body cavity, occupying half the body length. Its duct projects posteriorly from the glandular tissue for about 0.25 mm.

### *Retractor muscles*

The pharyngeal and tentacular retractors are not separated, as in *Arion*, but have a common origin from the posterior edge of the diaphragm in the middle line. At the posterior border of the kidney this divides into the pharyngeal retractor, which is bifurcate for about one-third of its length, and the tentacular retractor. The latter soon divides into right and left branches, and these divide again much further forward into branches to the upper and lower tentacles. The penial retractor arises further forward, on the left side of the diaphragm.



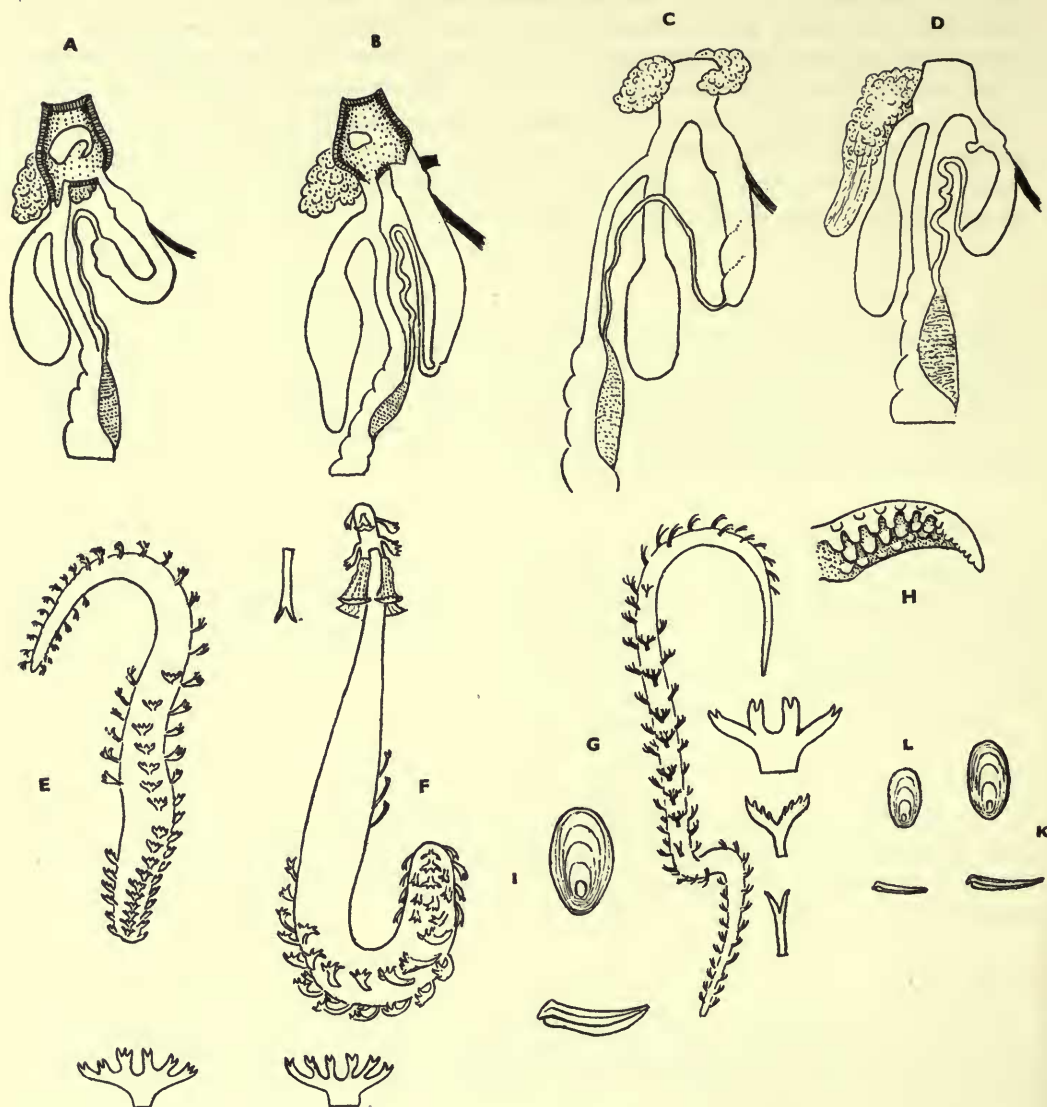


FIG. 8. *Milax*. Distal genital ducts ( $\times 4$ ). A. *M. gagates*—atrium opened to show stimulator. B. *M. sowerbyi*—atrium opened to show stimulator. C. *M. budapestensis*. D. *M. cf. insularis*.

Spermatophore ( $\times 6.7$ ), spines ( $\times 33$ ). E. *M. gagates*—one spine. F. *M. sowerbyi*—two spines. G. *M. budapestensis*—three spines.

H. *M. cf. insularis*—papillate stimulator.

Shell ( $\times 2.7$ ), dorsal and lateral views. I. *M. sowerbyi*. K. *M. gagates*. L. *M. budapestensis*.

*Nervous system*

The cerebral ganglia are connected by a short broad commissure. The cerebro-pleural and cerebro-pedal commissures are short, so that the nerve ring closely surrounds the oesophagus. The pleural, visceral and abdominal ganglia are closely approximated, as are also the visceral and pedal ganglia. The abdominal ganglion is almost completely fused with the left visceral. There is little if any variation in the nervous system between the species of *Milax*.

*Jaw*

Brown, oxygnathous, measuring 1.7 mm across.

*Radula* (Text-fig. 9 A)

The central tooth has a mesocone and well-developed ectocones. The laterals have well-marked endo- and ectocones, nearly equal in size. Most of the marginals lose the ectocones, but five or six of the innermost teeth retain them. Formula C.17.27, with slight variation (see p. 157).

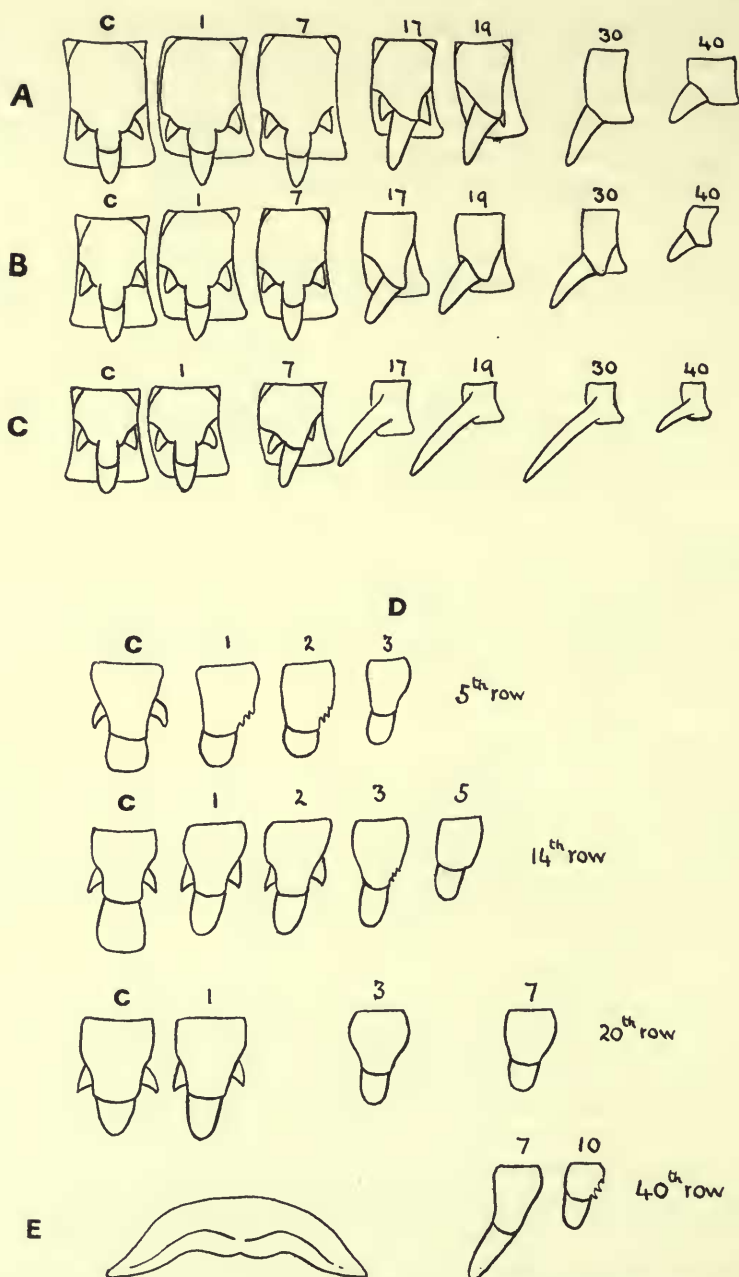
*Alimentary system*

The brown oesophagus leads to a long capacious crop, and the intestine (which exhibits marked spiral torsion) extends well behind the stomach, thus contrasting strongly with the condition in *Arion*. The rectum runs forwards above the common stem of the retractor muscles.

*Reproductive system* (Text-fig. 8 A)

The spiral ovotestis, mainly hidden by the upper lobes of the liver, gives off the pale hermaphrodite duct. This is much folded in its anterior wider part, and the terminal slender portion bears an oval seminal vesicle at its entry into the linguiform albumen gland. The common duct is long, voluminous and folded. The spermatheca is an oval sac, with a short duct arising from the oviduct 1.5 mm before its termination.

The prostate is a yellow ribbon-like organ on the common duct. At the beginning of the free oviduct it gives off the somewhat convoluted vas deferens, which enters the apex of the epiphallus. The epiphallus is widest apically and has a rounded eminence or blunt caecum below the apex, a feature that is not shared by *M. sowerbyi* or *M. budapestensis*. At the insertion of the retractor muscle, the epiphallus, without any external sign, passes into the penis, which narrows towards its termination in the atrium. Before its termination the penis shows two more or less distinct dilations, the upper one containing the blunt perforate penial papilla with a small pigmented diverticulum. The mucous membrane of the epiphallus is thrown into transverse circular folds, and that of the penis into longitudinal folds. A lobulated gland that can be unravelled into long glistening white tubules opens into the atrium. The atrium lodges a fleshy conical stimulator attached by its larger end, with the tip often folded back. The stimulator is generally smooth but occasionally has two or three minute papillae near the tip.

FIG. 9. Representative radular teeth ( $\times 330$ ).C. *M. budapestensis*.*M. sowerbyi*, an individual one day old.( $\times 1,000$ ).E. Jaw ( $\times 67$ ).A. *M. gagates*.B. *M. sowerbyi*.

D. Representative radular teeth

*Spermatophore* (Text-fig. 8 E)

A brown chitinous tube about 10 mm long, widest at the centre and narrowing at the anterior end. Except at two places on the concave side, it bears prominent spines throughout. The spines have four main branches, and fourteen or sixteen terminal points.

*Mating*

Observations are very scanty, but apparently the partners during coitus are in close contact, and little or nothing of the genitalia is visible. Though the stimulator is often found protuded in spirit specimens, it is not visible during coitus. Mating has been recorded in spring, summer and winter. Taylor describes the eggs as  $2 \times 1.5$  mm, transparent and thin shelled. This, if correct, is much smaller than the eggs of *M. sowerbyi* and *M. budapestensis*.

*Ecology*

Though widely distributed in the British Isles, *M. gagates* seems to be commoner near the sea than inland, and especially common in the south-west. In parts of Devon it is abundant in root crops, and can be a pest. It inhabits cliffs, wild places and gardens. In captivity, like most other slugs, it eats carrot, potato and oatmeal.

*Distribution* (Map 12)

*M. gagates* probably occurs in all the vice-counties of England, Wales and Ireland, the south of Scotland, the Isle of Man and the Clyde Islands. In Europe, its distribution is essentially north-western, though specimens from Marseilles have been examined. Other records from the Mediterranean area probably refer to a closely-related species, here distinguished as *M. cf. insularis* (p. 156).

*M. gagates* has been introduced into South Australia, Hawaii, California, Canary Isles and Trīstan d'Acunha. It is not yet clear whether other records of introductions into America, Bermuda, Ascension Island, St. Helena, South Africa, Australia, Tasmania, New Zealand and Polynesia refer to *M. gagates* or to *M. cf. insularis*.

*Fossil record*

Pleistocene to Recent.

*Material examined*

Living specimens from Epsom, Surrey; Southwell, Nottingham; Porthcawl, Glamorgan; Haverfordwest, Pembrokeshire; St. Agnes, Scilly Isles; and Majorca. Spirit specimens from Aberdeen, and from Marseilles, France; Santa Cruz, Teneriffe; Calbaden Canyon, Puente Hills, Los Angeles, California; Kensington suburb, Adelaide, South Australia (coll. B. C. Cotton); and Haleakala Maui, Hawaii.

*Milax* cf. *insularis* (Lessona & Pollonera, 1882)

*Amalia insularis* Lessona & Pollonera, 1882 : 57 (see 1884 : 103). Sardinia and Sicily.

*Amalia ichnusae* Lessona & Pollonera, 1882 : 60 (see 1884 : 106). Sardinia.

*Notes*

If the name *gagates* is to be reserved for the north-western species with the smooth stimulator (p. 149), the valid name for the present species remains to be determined. Several names whose application is uncertain (some of which are listed on p. 150) are available within the *gagates* complex. It will require a thorough study of the Mediterranean forms to clarify the biological and nomenclatural situation.

*First British record*

This is the first record to be published. Mr. Armitage collected specimens near Bexhill, Sussex, about 1948, and the differences between these and *M. gagates* were confirmed by Mr. Watson (*in litt.*). All other specimens examined, from various parts of Britain, have proved to be *M. gagates*.

*Diagnostic features*

Differs from *M. gagates* in having large papillae on the atrial stimulator. Also, the slug is usually larger, blacker and less smooth, with a darker sole.

*External appearance*

As *M. gagates*, except for the usually larger size, more prominent tubercles, and more intensely black coloration, with the sole not conspicuously paler.

*External variation*

It is not at present possible to assign named varieties to this poorly understood species.

*Shell, pallial organs, pedal gland, retractor muscles, nervous system*

As in *M. gagates*, as far as is known.

*Jaw*

As in *M. gagates*, though varying from pale brown to nearly black in the material examined.

*Radula*

The teeth closely resemble those of *M. gagates* in form and number. Formulae of radulae examined were : *M. cf. insularis* C.18.28 (Catania, Sicily), C.17.28 × 105



and C.19.27 (Malta), C.20.30  $\times$  102 (Marseilles); *M. gagates* C.15.31  $\times$  100 (Aberdeen), C.16.27 (Porthcawl), C.17.27  $\times$  96 (California), C.19.27  $\times$  102 (Marseilles).

#### *Alimentary system*

As in *M. gagates*.

#### *Reproductive system* (Text-fig. 8 D)

Here the differences from *M. gagates* are obvious. The stimulator (Text-fig. 8 H), instead of being smooth or having at the most two or three minute papillae near the tip, has large papillae disposed in four longitudinal rows near the base, diminishing to two rows and becoming smaller towards the apex. Sometimes the papillae are mucronate, and in one specimen they were found to be partly retracted. The atrial glands extend further backwards than in *M. gagates*, in a tongue-like prolongation.

The epiphallus does not possess the sub-apical bulge seen in *M. gagates*. The small internally-pigmented accessory penial papilla, instead of being enclosed in the penis sheath, bulges externally; but it seems likely that this character varies with the physiological state of the animal, in both species.

Whereas Mediterranean specimens examined had four rows of papillae towards the bases of their stimulators, Lessona & Pollonera (1884, pl. 2, figs. 1 and 2; 6 and 7) figure "*gagates*" and *insularis* with only two rows. They describe *ichnusae* as having a single row of papillae, though their figure shows the stimulator as smooth (1884: 106 and pl. 2, fig. 4). Possibly there is more than one species with a papillate stimulator in the Mediterranean region. Mr. Aten of Zaandam, Holland, reports (*in litt.*) finding *M. gagates* and *M. cf. insularis* in the Pyrenées Orientales, and that the latter when young has only a single row of papillae. This suggests that *M. ichnusae* may be an immature form.

#### *Spermatophore, mating, development, behaviour, ecology*

Not known.

#### *Distribution*

In Britain, once recorded from Bexhill, Sussex. In Europe, found in the Mediterranean region. Occurs together with *M. gagates* near Marseilles.

#### *Fossil record*

Not distinguishable from *M. gagates*.

#### *Specimens examined*

Spirit specimens from Marseilles and Valence, Malta, Sicily and Majorca.

*Milax sowerbyi* (Férussac, 1823)

*Limax sowerbyi* Férussac, 1823, 2 : 96, pl. 8. London.

*Limax carinatus* Risso, 1826 : 56.

*Limax marginatus* Jefferies, 1862 : 132.

*Amalia maculata* Collinge, 1895b : 336, pl. 23, fig. 6.

*Amalia collingei* Hesse, 1926 : 139.

*First British record*

By Férussac (1823).

*Diagnostic features*

Differs from *M. gagates* in brown colour speckled with darker patches, pale keel and margin of respiratory orifice, grooves between tubercles pigmented, keel not abruptly truncated, animal less compressed laterally when contracted, mucus yellow and more tenacious. Differs from *M. budapestensis* in broader, uniformly pale sole.

Internally characterized by short blunt atrial stimulator, long conical spermatheca, tapered spermatophore hooked at blunt end and bare of spines at narrow end.

*External appearance* (Pl. 2, fig. 23)

Length when extended about 7 cm. When contracted the slug is rather less compressed laterally than *M. gagates*, and the keel is not abruptly truncated behind. The body is usually pale or dark brown with darker speckling, with the keel paler and the grooves between the tubercles pigmented. The mantle grooves are as in *M. gagates*, but the respiratory orifice is pale margined. The tripartite sole is pale, and the sticky mucus yellow.

*Variation*

Var. *alba* Taylor (1904), entirely white ; var. *fuscocarinata* Cockerell (1886c), keel the same colour as the back ; var. *nigrescens* Cockerell, black with orange keel ; var. *oretea* Lessona & Pollonera (1882), with median dark streak on mantle—found in Devon and Glamorgan.

*Shell* (Text-fig. 81)

Larger, thicker and more evenly oval than that of *M. gagates*, measuring  $5 \times 3$  mm.

*Pallial organs*

As in *M. gagates*.

*Pedal gland*

The duct does not project beyond the glandular tissue.

*Retractor muscles*

The pharyngeal retractor is more deeply cleft than in *M. gagates*, and the two tentacular retractors separate sooner. The penial retractor arises nearer to the

common stem of the other muscles, and there is a pair of short muscles from the penis to the body-wall.

#### *Nervous system*

As in *M. gagates*.

#### *Jaw*

As in *M. gagates*, but a little broader from upper to lower margin.

#### *Radula* (Text-fig. 9 B)

As in *M. gagates*, except that there are a few more transverse rows of teeth, and there are fewer laterals and more marginals in each row, with two or three of the innermost or transitional marginals often retaining a minute ectocone. Formula C.13.36  $\times$  115.

#### *Alimentary system*

As in *M. gagates*.

#### *Reproductive system* (Text-fig. 8 B)

The lower genital ducts differ from those of *M. gagates* in several features. The short wide spermatheca duct arises from the free oviduct even nearer the atrium, and the sac has a narrowing backward prolongation. The epiphallus widens instead of narrowing towards its termination, and does not present the sub-apical lateral bulge of *M. gagates*, nor the small pigmented diverticulum at the distal end of the penis. The atrium contains a short blunt smooth stimulator.

#### *Spermatophore* (Text-fig. 8 F)

Thicker than in *M. gagates*, measures about 13 mm long. The thinner anterior end is smooth, and the curved posterior end bears recurved spines of three types. As usually found in the spermatheca, and figured by Taylor (1902-07, fig. 174) and others, the smooth anterior end terminates abruptly. However, if the spermatophore is taken very shortly after coitus, before the spermathecal fluid has had time to act upon it, the anterior end is found to be capped by a curious conical structure about 2 mm long, with a rounded apex, and formed by four leaflets with fringed edges (Quick, 1950). A fresh spermatophore of *M. budapestensis* does not have this cap, but no opportunity has occurred of examining a fresh spermatophore from *M. gagates*. Occasionally two spermatophores are found in the spermatheca in *M. sowerbyi*, but whether they are transferred during a single coitus (which is very prolonged) or on two separate occasions is not known.

#### *Mating*

After following and then curving around, the pair remain in close contact for twelve to eighteen hours, and little or nothing is visible of the genitalia. Pairing has been observed in October and November, but perhaps occurs at other times.

*Development*

The eggs are  $4 \times 3.5$  mm, soft, translucent and pale amber, laid in clusters of about a dozen, hatching in from four to six weeks. The embryo before hatching has a large flattened caudal vesicle nearly circular in outline. When hatched the young are 8 mm long, with a conspicuous pale keel. The mantle is speckled with black and sometimes has a dark median streak, which is retained in var. *oretea* when adult.

*Ecology*

*M. sowerbyi* is found in gardens, cultivated fields and rubbish heaps. It burrows in the ground, and can do considerable damage to carrot and potato crops.

*Distribution* (Map 13)

Occurs in probably every vice-county of England, Wales, Ireland and the southern half of Scotland, and in France, Belgium and Spain. Probably known under other names from Portugal, Italy, Greece and the north coast of Africa. Introduced into South America and New Zealand?

*Fossil record*

Pleistocene to Recent.

*Material examined*

Living specimens from many places in Glamorgan, Pembroke, Surrey, Berkshire and Sussex. Spirit material from Britain and Marseilles.

*Milax budapestensis* (Hazay, 1881)

*Limax gracilis* Leydig, 1876 : 276, nec *Limax gracilis* Rafinesque-Schmaltz, 1820a.

*Amalia budapestensis* Hazay, 1881 : 40. Budapest.

*First British record*

By Phillips & Watson (1930).

*Diagnostic features*

Sole with dark central and paler lateral areas; body when contracted tends to lie in a curve and is less compact and humped than *M. gagates* and *M. sowerbyi*. No atrial stimulator, spermatophore slender and spirally twisted. Radula has more marginal teeth, and spermathecal duct is longer, than in *M. gagates* and *M. sowerbyi*.

*External appearance* (Pl. 2, fig. 20)

The smallest British species of *Milax*, very slender when extended to 5 cm. The dorsum is dark, sometimes nearly black or with a brownish tinge, with a dirty

yellow or orange keel. The grooves between the dorsal and the lateral, somewhat polygonal, tubercles are deeply pigmented. The mantle is sometimes paler than the dorsum, the horseshoe-shaped groove deeply pigmented, and the small respiratory orifice has a grey margin. The peripodial groove and margin of the sole are deeply pigmented, the lateral areas of the sole grey, and the median area dark grey or nearly black. The mucus is viscid and colourless, but in the mantle area becomes yellowish after repeated irritation.

#### *External variation*

Variation is confined to the intensity of the general grey colour ; to the tint of the keel, which varies from yellow to brownish-orange ; and to the sole, whose lateral areas are occasionally darker than the central area.

#### *Shell* (Text-fig. 8 L)

Concave or flat below, measuring  $3 \times 1.25$  mm, brownish in colour.

#### *Pallial organs*

As in *M. gagates*.

#### *Pedal gland*

The duct extends behind the glandular tissue for about 5 mm.

#### *Retractor muscles*

The tentacular and pharyngeal retractors are usually rather more deeply cleft than in *M. gagates*, less so than in *M. sowerbyi*.

#### *Nervous system*

As in *M. gagates*.

#### *Jaw*

Brown and oxygnathous as in the other species but smaller, measuring about 1.5 mm across and 0.5 mm in height.

#### *Radula*

Differs from those of the other species in having the basal plate of the central tooth relatively broader, the aculeate mesocones of the marginals more slender, fewer lateral teeth and more marginals. Formula C.7-8.38-40.

#### *Alimentary system*

As in *M. gagates*.

#### *Reproductive system* (Text-fig. 8 c)

The pale spirally twisted ovotestis has five or six closely approximated lobes,



each composed of numerous follicles. The hermaphrodite duct is slender for the greater part of its length, but becomes dilated and folded near the albumen gland, and here shows a small seminal vesicle. The common duct with a broad yellow prostatic ribbon is folded S-wise, and after parting from the vas deferens contracts to form a relatively long slender free oviduct. At about two-thirds of its length, the wider relatively long spermatheca duct arises, leading to a cylindrical sac with a rounded apex. The rather long flexuous vas deferens enters the epiphallus sub-apically. In the writer's experience the epiphallus and penis are long and slender, but Phillips & Watson (1930) describe and figure a short blunt form in addition, and find this the commoner. It is not known if this is a true dimorphism, or only the result of the physiological condition. Hazay (1881, pl. 1) shows an intermediate form of penis and epiphallus, and Simroth (1885, pl. 10, fig. 13) the long form. Both forms occur in Belgian specimens, sent to me by Dr. W. Adam. The atrium receives the slender ducts of a pair of lobulated atrial glands, and has no stimulator.

### *Spermatophore* (Text-fig. 8 G)

Length about 16 mm, anterior end slender, posterior end spirally twisted. No trace of a frilled cap as in *M. sowerbyi*, even in spermatophores removed during or immediately after coitus. Except for the first 2 mm at the anterior end, the spermatophore is covered by forwardly-recurved branching spines, which are smaller and less branched towards the ends. There are two rows of spines anteriorly, three or four rows on the posterior two-thirds.

### *Mating*

Occurs during November, December and January, under cover of loose stones or logs. Coitus generally starts in the evening and continues until the following mid-day or later. A little of the partly everted atria and the two penes is visible between the necks of the partners. The atrial glands are partly contained in the everted atria, together with the distal ends of the genital ducts.

### *Development*

The ellipsoidal yellow leathery eggs are laid in small clusters underground, and measure  $2.9 \times 2.25$  mm. Those laid in December hatch in March. The young at hatching are 4.5 mm long, pale yellowish-grey with a recognizable keel.

### *Behaviour*

Whereas when at rest the other species of *Milax* assume a compressed helmet shape, *M. budapestensis* is usually found only half contracted, and curved into a semicircle.

### *Ecology*

Occurs mostly in gardens and allotments, under stones and rubbish, and can do considerable damage to roots and tubers. Though much less common in wild places, there are records for such situations in Wales and Cheshire.

*Distribution* (Map 14)

Recorded from many localities in the British Isles, mainly in western England and Wales, but also in south-eastern England, southern Ireland and the Hebrides. On the Continent, known from Belgium, Germany (Württemberg, Tübingen, the Rhön Mountains and Würzburg), North Italy (Verona, Vicenza and Padua), Hungary (Budapest), Transylvania, Bulgaria and Crimea. It probably occurs in many places between these widely-separated localities, in the zone from the British Isles to the Crimea. For a map and further details, see Phillips & Watson (1930) and Ellis (1951).

*Fossil record*

Recent.

*Material examined*

Living specimens from Berkshire, Glamorgan, Pembroke and Denbighshire. Spirit material from Britain and Belgium.

## Subfamily LIMACINAE

Limacidae in which the keel rarely extends forwards as far as the mantle. The nucleus of the enclosed shell is terminal and lies to the left of the mid-line. The mantle is concentrically ridged and lacks a horseshoe-shaped furrow. There is no well-developed epiphallus, no spermatophore and no atrial gland. The stimulatory organ, when present, is a penial sarcobelum, and not an atrial stimulator as in *Milax*. The endocones of the lateral radular teeth, when present, are more or less united with the mesocones. The intestine has one or two forwardly-directed loops.

Genus *AGRIOLIMAX* Mörch, 1865

Type species *Limax agrestis* Linnaeus, 1758.

The right ocular retractor lies to the left of both penis and vagina. The intestine has one forwardly-directed loop, and the right lobe of the liver forms the apex of the visceral mass. A penial sarcobelum is present, more or less developed. The nucleus of the concentric mantle ridges lies to the right of the middle line, over the respiratory orifice. The tail is obliquely truncate.

Pilsbry (1944, 1948) adopts the name *Deroceras* Rafinesque-Schmaltz (1820a : 10) for this genus, as do most American and many European authors. Watson (1943 : 54) discusses the question. Ellis (in press) has submitted to the International Commission on Zoological Nomenclature a proposal for the suppression of *Deroceras* and other older names, and the validation of *Agriolimax*.

Hesse (1926) mentions sectional names for the first three species considered here. *Agriolimax* s.s. (including *A. agrestis* and *A. reticulatus*) has a rectal caecum and

a more or less tufted penial appendix, whereas *Hydrolimax* Malm (including *A. laevis*) lacks both caecum and appendix, but has a long tubular penial diverticulum. Other sectional names have been proposed for groups of extra-limital species, such as *Krynickyllus* Kaleniczenko, which lacks caecum, appendix and sarcobelum. However, several species show combinations of characters not covered by existing sectional names. *A. caruanae* has a tufted penial appendix like *Agriolimax* s.s., but lacks a rectal caecum like *Hydrolimax*; while one or both of its penial diverticula may correspond to the latter's single but minutely bifid diverticulum. A slug collected in Cyprus by A. R. Waterston (? *A. cyprius* Simroth, 1906, or *A. panormitanus* Lessona & Pollonera, 1882) has a tufted appendix and a single diverticulum. Of two Abyssinian slugs described by Quick (1954), *A. gughensis* lacks caecum, appendix and diverticula but has a long, narrow, backwardly-directed sarcobelum; while *A. scotti* lacks caecum, appendix and sarcobelum, but has two diverticula. In view of the intergradation and overlapping between species of which the anatomy is known, and of the number of species (especially in south-eastern Europe) of which it is not known, the use of sectional names within this genus does not seem useful.

### *Agriolimax reticulatus* (Müller, 1774)

*Limax reticulatus* Müller, 1774 : 10. Denmark.

*Limax canariensis* d'Orbigny, 1839 : 47.

*Krynickyllus minutus* Kalenickzenko, 1851 : 224.

#### Notes

The name *agrestis* has been used for this species by most British authors (see p. 170).

#### First British record

By Lister (1674 : 99).

#### Diagnostic features

Distinguished from *A. laevis* and *A. caruanae* by larger size, opaque appearance with very variable coloration, white sticky mucus and less active movements; and internally by the presence of a rectal caecum. Differs from *A. agrestis* in the trifid crenulate penial appendix, and the posterior situation of the ovotestis.

#### External appearance (Pl. 2, fig. 15)

Length about 3.5 cm. The tail is obliquely truncated, the back keeled for a short distance at the hind end, and the sole tripartite. The respiratory orifice is at about two-thirds of the distance from front to back of the mantle, and the reproductive orifice close behind and below the right upper tentacle. The concentric striae of the mantle disappear in alcohol. The mucus is whitish on account of calcareous granules.

The colour is variable, with the body usually marked with brown or grey. The respiratory orifice has a conspicuous pale border.

### *External variation*

The colour varies from pale cream to bluish-black, but is usually some shade of brownish-yellow, with darker grooves and scattered dark brown markings of varied shapes and sizes. Named varieties and subvarieties are very numerous. Many are practically synonymous, while some of those listed by Taylor (1902-07) refer to other species. Individuals often become darker as winter approaches. The following varieties may be recognized: var. *cineracea* Moquin-Tandon (1855), entirely ash coloured; var. *violacea* Gassies (1849), lilac or slate-coloured; var. *rufescens* Dumont & Mortillet (1856), rufous; var. *reticulata* Müller (1774), grooves dark, giving a reticulate appearance; var. *nigra* Morelet (1845), black, with pigment sometimes invading the sole. Albino forms occur occasionally.

### *Shell* (Text-fig. 10 F)

The right border is convex.

### *Pallial organs* (Text-fig. 10 A)

When the mantle is reflected to the right, a lobe of the kidney is seen to cover the rectum, and the short retractor penis to arise from the diaphragm at the anterior border of the pericardium.

### *Retractor muscles* (Text-figs. 11 G and H)

The cephalic retractor muscles arise as a single stem in the mid-line, a short distance behind the diaphragm. The main stem usually divides basally, to form the right ocular retractor, and a common stem for the left ocular and the buccal bulb retractors (Text-fig. 11 G), but variations occur (Text-fig. 11 H). The genital retractor arises from the diaphragm near the front of the kidney, and is inserted between the vas deferens and the constriction above the sarcobelum.

### *Nervous system*

This is very similar to that of *Milax*.

### *Jaw*

Pale golden, of the usual oxygnathous type.

### *Radula* (Text-figs. 11 L and O)

As in all *Agriolimax*, the endocones of the lateral teeth are delicate, lying close to the mesocone and on a slightly more superficial plane. The basal plates of the central and lateral teeth are larger and relatively narrower than those of *A. agrestis*.

Table I compares the radulae of the four British species of *Agriolimax*.



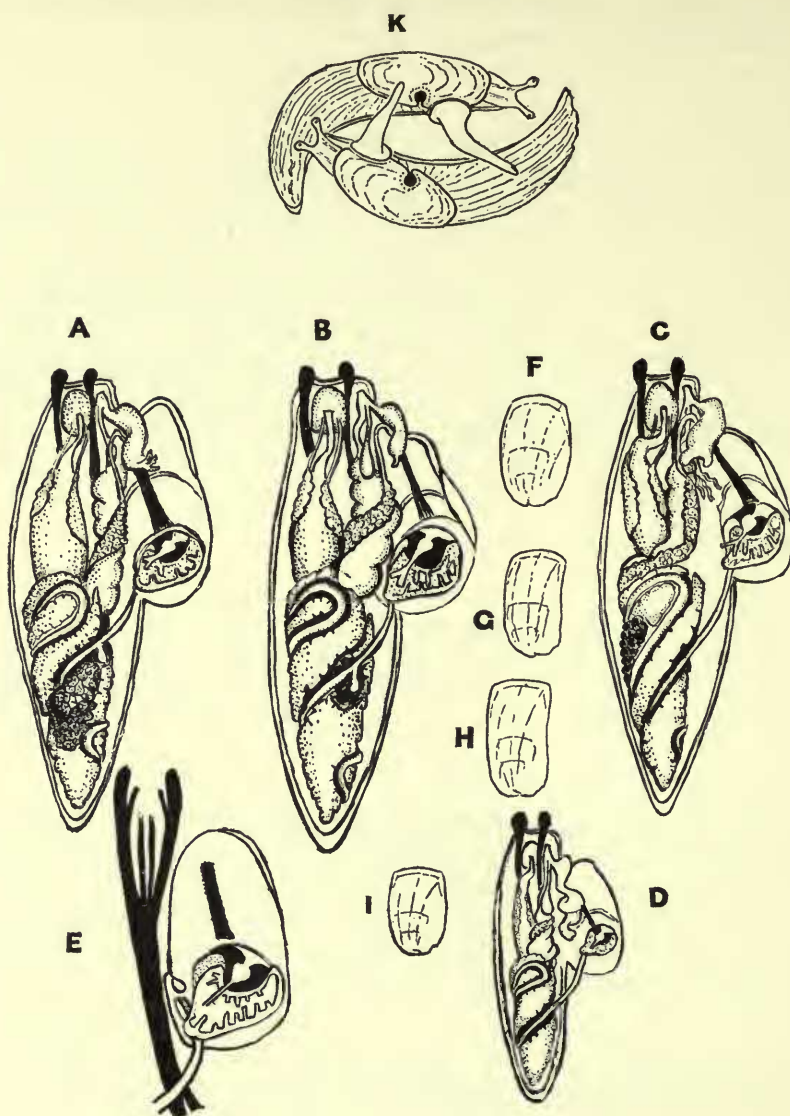


FIG. 10. *Agriolimax*. Dissection with mantle reflected to the right. A. *A. reticulatus*—( $\times 2$ ), ovotestis extends much further backwards than in *A. agrestis*. B. *A. agrestis*—( $\times 2$ ), ovotestis does not extend much further back than the rectal caecum. C. *A. caruanae*—( $\times 2.7$ ), ovotestis far forwards, exposed on left side. No rectal caecum. D. *A. laevis*—( $\times 2.7$ ).

*A. caruanae*. E. Pallial region and cephalic retractors ( $\times 12$ ). K. Mating pair with sarcobela protruded.

Shell ( $\times 4$ ). F. *A. reticulatus*. G. *A. agrestis*. H. *A. caruanae*. I. *A. laevis*.



TABLE I.—*Radular Formulae of the British Species of Agriolimax Mörch*

Locality	Date	Formula	Central tooth (mm)	Remarks
<i>Agriolimax reticulatus</i> (Müller)				
Capel-y-ffin, Brecknock	20.vii.46	C.14.22 × 86	0.043 × 0.022	—
	20.vii.46	C.17.27 × 107	?	—
Blackpill, Swansea	17.viii.46	C.14.22 × 88	?	Small but mature.
Mumbles Rd., Swansea	23.viii.46	C.14.21 × 100	0.035 × 0.017	—
Porteynon, Glamorgan	? .xi.31	C.16.22	0.049 × 0.024	—
Clyne Valley, Swansea	7.ix.46	C.17.26 × 100	0.043 × 0.022	—
Llanwrtyd Wells	18.xi.38	C.6.8	—	Young, 8 mm long.
Burpham, Surrey	29.xii.46	C.18.26 × 122	0.052 × 0.026	—
<i>Agriolimax agrestis</i> (Linnaeus)				
Wheatfen Broad	17.viii.46	C.16.23	0.038 × 0.019	Radula 3.2 × 1.7 mm.
	23.viii.46	C.16.23 × 105	0.040 × 0.02	—
	17.viii.46	C.14.21 × 100	0.034 × 0.017	—
	? .x.46	C.15.24	0.038 × 0.019	—
	? .ix.46	C.15.?	0.035 × 0.017	—
	?	C.15.21 × 100	0.032 × 0.016	—
<i>Agriolimax laevis</i> (Müller)				
Singleton, Swansea	10.iii.48	C.13.27 × 92	0.023 × 0.012	Euphallic.
	2.viii.48	C.13.25 × 95	0.023 × 0.012	Hemiphalllic.
<i>Agriolimax caruanae</i> Pollonera				
Sketty, Swansea	? .x.31	C.14.50	—	—
	? .iv.32	C.14.55	—	—
Singleton, Swansea	31.i.35	C.10.?	0.023 × 0.014	Young, 12 mm.
Porteynon, Glamorgan	? .vii.46	C.14.55 × 118	0.029 × 0.017	Radula 3.1 × 1.5 mm.

*Alimentary system* (Text-fig. 10 A)

The lobulated salivary glands lie on each side of the crop, which narrows as it enters the small stomach. The posterior loop of the intestine extends behind the stomach towards the apex of the visceral mass, which is formed by the right lobe of the liver. The rectum has a small caecum overlying the ovotestis.

*Reproductive system* (Text-fig. 11 C)

The brown lobulated ovotestis lies towards the rear of the visceral mass, and is partly exposed on the surface (Text-fig. 10 A). The hermaphrodite duct is short and only slightly sinuous, with a seminal vesicle at its slender termination where it enters the albumen gland. The latter is short, shaped like a mammalian liver, and

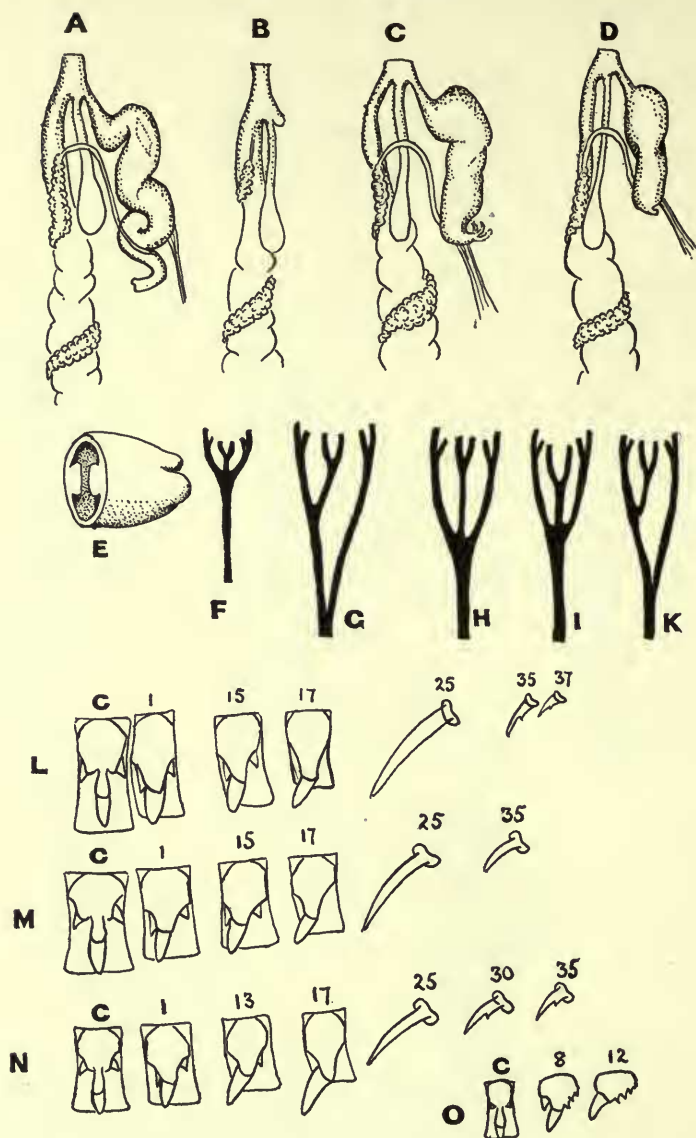


FIG. 11. *Agriolimax*. Distal genital ducts ( $\times 5.3$ ). A. *A. laevis*—euphallic individual. B. *A. laevis*—aphallic individual. C. *A. reticulatus*. D. *A. agrestis*.

E. *A. laevis*—apex of penial appendage, showing bifid tip and two pilasters.

Cephalic retractor muscles. F. *A. laevis*. G & H. *A. reticulatus*. I & K. *A. agrestis*.

Representative radular teeth. L. *A. reticulatus*—( $\times 330$ ). M. *A. agrestis*—( $\times 330$ ). N. *A. laevis*—( $\times 330$ ). O. *A. reticulatus*—( $\times 500$ ) from young animal 8 mm long.

pale brown in colour. The common duct, with the lobulated prostatic ribbon, is thrown into zig-zag folds. The free oviduct is short and straight, and the atrium small. The spermatheca duct arises from the atrium and expands to a narrow oval sac. The short vas deferens enters the penis beyond its apex, beneath the genital retractor muscle. The penis is narrow basally, expands to a segment containing the triangular sarcobelum, and narrows a little before the apical segment. The latter terminates in a large penial appendage which is trifid, each branch having a crenulated outline. The details of the branching vary to some extent. The branches, which are tubular, are everted and turned completely inside out during mating, as in *A. agrestis* and *A. caruanae* (see Text-figs. 12 D and E).

### *Mating*

This can occur throughout the year in Britain, even in the winter months, taking place on the surface usually after dark. The pair follow one another for from half to one hour in a narrowing circle, with copious exudation of mucus. The sarcobelum is protruded and plays over the partner's body. Then the animals remain still, neck to neck with bodies curved, and each atrium and penis is everted, bringing the oviduct and spermatheca duct to the surface. Then the base of the penial appendix appears and is explosively turned inside out, the branches appearing as long thin hyaline threads. A mass of sperms enclosed in a ball of mucus is simultaneously transferred from one partner to the other's everted mass, to which it adheres. The animals separate at once, and in a few seconds the genital complexes are invaginated and withdrawn, carrying the sperm packets with them.

### *Development*

The eggs, laid about ten days after mating, are about  $3 \times 2.5$  mm, translucent and speckled with calcareous dots which become absorbed during development. They hatch in two or three weeks, the young being 4 mm long, pale grey and translucent, and like all the British species have no bands at any stage. The young grow rapidly, and in warm weather may mature in three months. During late embryonic development the caudal and cephalic vesicles can be seen pulsating through the translucent shell, when the eggs are viewed under water (see Text-fig. 18 G). In Britain several broods are produced by a pair, and 700 eggs may be produced in a season. Luther (1915) states that self-fertilization occurs in *A. reticulatus* isolated from birth.

### *Ecology*

*A. reticulatus* is perhaps the commonest British slug. It prefers drier sites than *A. agrestis* and occurs in grass fields, root crops, hedges, gardens and rubbish heaps, and under stones and logs in woods and coppices. It is often a serious pest in gardens and allotments, devouring seedlings and green crops.

### *Distribution* (Map 15)

Ubiquitous in the British Isles. Probably indigenous to most of Europe, the

Mediterranean region and the Atlantic isles, and introduced by commerce into most parts of the world.

*Fossil record*

Pleistocene to Recent.

*Material examined*

Living specimens from many places in England and Wales. Spirit material from Britain, Europe, Atlantic isles, Réunion, America and New Zealand.

***Agriolimax agrestis* (Linnaeus, 1758)**

*Limax agrestis* Linnaeus, 1758 : 652. Sweden.

*Limax bilobatus* Férussac, 1819 : 74.

*Limax pallidus* Schrenk, 1848 : 143.

*Notes*

The commonest British slug, *A. reticulatus* (Müller), was formerly regarded by British authors as a variety of *A. agrestis*, though Luther (1915) had shown them to be distinct. It is uncertain which of many synonyms in this group of slugs belong to *A. agrestis* and which to *A. reticulatus*.

*First British record*

By Ellis (1941). The slug was found at Wheatfen Broad, Norfolk, and determined by H. Watson.

*Diagnostic features*

Agrees externally with *A. reticulatus*, except that it is smaller, smoother and more slender and seldom has more than a few small dark flecks. Internally, the ovotestis lies further forward, and the penial appendix is short, smooth and unbranched.

*External appearance*

Like *A. reticulatus*, but rather slimmer and smoother, and less pigmented. The body is pale greyish-yellow, paler on the sides, sometimes with whitish calcareous-looking spots.

*External variation*

Occasionally, a few dark flecks are present and the grooves are slightly pigmented.

*Shell* (Text-fig. 10 G)

About 3 mm long, usually with the right border slightly concave.

*Pallial organs* (Text-fig. 10 B), *retractor muscles* (Text-figs. 11 I and K), *nervous system, jaw*

As in *A. reticulatus*.

*Radula* (Text-fig. 11 M)

The teeth are a little smaller than in *A. reticulatus*, and the basal plate wider (Table I, p. 167).

*Alimentary system* (Text-fig. 10 B)

As in *A. reticulatus*.

*Reproductive system* (Text-fig. 11 D)

The ovotestis lies further forward than in *A. reticulatus*, near the centre of the visceral mass, and is only partly exposed on the right side beneath the rectal caecum (Text-fig. 10 B). The remainder of the reproductive system is like that of *A. reticulatus*, except for the apex of the penis, which terminates in a single small curved digitiform appendix.

*Mating*

As in *A. reticulatus*. Mating occurs in Britain in the autumn, and perhaps at other times. Luther (1915) states that this species is incapable of self-fertilization, unlike *A. reticulatus*.

*Development*

The eggs are laid in clusters of from ten to twenty or more. They measure from  $2.2 \times 2.0$  to  $2.5 \times 2.25$  mm, and are more translucent and more finely dotted with calcareous particles than those of *A. reticulatus*. The newly hatched young are 3.5 mm long, translucent and whitish, and have no bands at any stage.

In Britain, the eggs are laid in the autumn and hatch in three or four weeks. The young mature in the following summer and autumn, and die in the late autumn after mating. In Finland, the life cycle is different (Luther, 1915), in relation to the more severe climate. The eggs are laid, and the parents die, in late August or September, while the eggs do not hatch until the following June. Thus embryonic life lasts for more than eight months in Finland and less than a month in England, while post-embryonic life lasts about three and twelve months respectively.

*Ecology*

In Britain, apparently confined to marshy carr (see Ellis, 1941) in East Anglia.

*Distribution* (Map 16)

In Britain, certainly recorded only from marshes by the Norfolk Broads: a single record of an immature specimen from North Uist (Ellis, 1951: 196) has not been confirmed. Probably widespread in Europe, northwards to Finmark and Iceland,



though the detailed distribution is uncertain because of confusion between this species and *A. reticulatus*. For example, Germain (1930) describes and figures *A. reticulatus* under the name *agrestis*.

### *Material examined*

Living specimens from Wheatfen Broad, Sutton Broad and Alderfen Broad, all in east Norfolk.

### *Agriolimax laevis* (Müller, 1774)

*Limax laevis* Müller, 1774 : 1. Frederiksdal, Denmark.

*Limax brunneus* Draparnaud, 1801 : 104.

*Limax campestris* Binney, 1844 : 52.

*Limax hyperboreus* Westerlund, 1876 : 97.

*Agriolimax bevenoti* Collinge, 1897c : 295.

### *Notes*

Müller described his slug as "totum nigrum", except for the median area of the sole, and compared its general appearance with that of the black land planarian *Rhynchodemus terrestris*. However, topotypes from Frederiksdal agree with the common slug, known as *A. laevis* in Britain, Europe and North America, in being some shade of brown. The discrepancy in colour is not highly significant, since the present species becomes very dark when somewhat dry and contracted, and since in America it varies in colour from amber to black (Pilsbry, 1948 : 540, 548 ; Altena, 1958 : 30).

Simroth (1885 : 222, pl. 9) described and figured, as forms of *A. laevis* from Germany, what are evidently representatives of two distinct species : those corresponding to the euphallic and aphyallic forms of the widespread slug (his figs. 21 G and 22 H), and a larger and darker species with a hammer-headed penis (his figs. 17 C and 18 D). The latter is found principally in Germany and Poland, though it appears to have been introduced to Gotland Island, Sweden (Lohmander, *in litt.*). It has never been recorded from Denmark and Lohmander, despite his considerable experience of Danish slugs, has never found it there. Taylor's figures (1902-07, figs. 131 and 132), purporting to show the genitalia of British *A. laevis*, are copied from Simroth and show this second species.

It seems that the name *laevis* can properly be retained for the species to which it has long been applied. There is no reason to transfer it to the species with the hammer-headed penis, the correct name for which is uncertain.

### *First British record*

By Johnston (1838 : 154), as *Limax brunneus*.

### *Diagnostic features*

Small size, colour light or dark brown, smooth, active. Much smaller than *A. caruanae*. Head and neck extend further from the mantle than in *A. reticulatus*. Internally distinguished from the other species by its more sinuous penis, with a

tubular caecum or appendix, and the frequent occurrence of aphyallic specimens ; and from *A. reticulatus* and *A. agrestis* by the absence of a rectal caecum.

*External appearance* (Pl. 2, fig. 19)

Length 1.7–2.25 cm. Light or dark brown, translucent, sometimes greenish, more or less flecked with darker spots. The respiratory orifice is less conspicuously pale-bordered than in the other species. The head and neck are thrust further forward than in *A. reticulatus* and *A. agrestis*, so that the mantle is more centrally placed, and the mantle has fewer concentric ridges. The mucus is clear, not milky. The slug is very active, and crawls rapidly.

*External variation*

The ground colour varies from pale to dark brown, with more or less darker flecking on body and mantle. Pale and dark specimens occur together at all seasons. Named varieties are var. *lacustris* Bonelli (in Lessona & Pollonera, 1882) (= var. *maculata* Cockerell, 1886b), irregularly spotted with dark brown ; var. *grisea* Taylor (1904), grey or greenish-grey.

There is also marked genital polymorphism, with euphallic, hemiphallic and aphyallic individuals.

*Shell* (Text-fig. 10 I)

Relatively short and broad.

*Pallial organs* (Text-fig. 10 D)

As in *A. reticulatus*.

*Retractor muscles* (Text-fig. 11 F)

The cephallic retractor muscles arise by a long common stem, and so are less deeply divided than in the other species. The retractor penis is occasionally absent.

*Nervous system*

As in *A. reticulatus*.

*Jaw*

Pale golden, 1 mm across.

*Radula* (Text-fig. 11 N)

Rather fewer lateral teeth, and small ectocones on more of the external marginals, than in *A. reticulatus* and *A. agrestis*. Formula C.13.26.

*Alimentary system*

The rectum lacks a caecal diverticulum, as in *A. caruanae*. The visceral cavity is often somewhat pigmented, though less so than in *A. caruanae*.

*Reproductive system* (Text-figs. 11 A and B)

The dark ovotestis is less exposed than in the other species. The hermaphrodite duct is short and nearly straight, with the usual seminal vesicle at the short brown albumen gland. The female portion of the common duct is leaden grey, and the prostate yellow. The spermatheca is normally oval as in the other species, but sometimes in young examples it is globular. The penis in a euphallic individual shows four regions: a distal, narrower segment; a wider one enclosing the triangular sarcobelum; a twisted and contorted segment entered distally by the vas deferens, and giving attachment to the retractor penis; and a short narrower segment (diverticulum or appendix), more or less bifid at the tip. The appendix contains two thickened pilasters, which fade out on reaching the sarcobelar segment. In the aphyallic form (Text-fig. 11 B) prostate and spermatozoa are present, but the vas deferens fades out or ends in a little vesicle, before reaching a minute knob representing the penis. Apparently the penis is always the last part to be fully developed; but in young examples that will become euphallic the vas deferens does reach the small penis and a retractor muscle is often present. Stages can be found between this and the adult euphallic form. Babor (1894) records observations which he thought indicated that *A. laevis* was normally protogynous—young adults being always female and middle-aged adults hermaphrodite, with some old animals attaining a purely male phase, with atrophied albumen gland and spermatheca and hypertrophied penis. He states that in the young stages sperms are very few, and there is no sperm duct or penis. However, dissection of many British examples, taken at various sites and different seasons, shows that here sperms, prostate and vas deferens are always present; though in animals that will eventually be aphyallic the vas deferens ends blindly. No example has been seen in which the albumen gland and spermatheca have atrophied. As these forms often occur together, in varying proportions in the same site at different seasons, it seems more likely that this is a case of genital dimorphism, such as occurs in *Zonitoides*. To establish this with certainty it is desirable that samples should be taken from the same site each month for a year, but an opportunity to do this has not occurred. Pilsbry (1948: 539-552) gives numerous figures of similar dimorphism in the American forms of *A. laevis*.

*Mating*

Gerhardt (1939) says that following and circling around is omitted in *A. laevis*, and that the partners remain in contact before the sperms are transferred for a much longer period (up to an hour) than in the other species.

*Development*

The eggs are laid singly or in small clusters, probably at all seasons of the year, having been found in January, April and October. They are relatively large, from  $1.8 \times 1.5$  to  $2 \times 1.3$  mm, translucent, resilient, finely punctate, with polygonal calcareous granules. They hatch in four or five weeks. The young are 4 mm long, white and translucent, with the opaque white liver lobes showing through the integument. The head and tentacles are light pinkish-brown with a violet tinge.

After a few days, pigmentation begins at the tail and head, and gradually invades the rest of the body.

### *Ecology*

*A. laevis* inhabits damper sites than our other slugs and is common in marshes and on the borders of ponds and rivers, but is occasionally found in drier sites, in fields and on the borders of woods. It has been seen feeding on mealy bugs infesting *Streptocarpus* in greenhouses.

### *Distribution* (Map 17)

Probably ubiquitous in the British Isles. Its continental distribution is somewhat uncertain, because of the existence of a somewhat similar slug distinguished by a hammer-headed penis (p. 172). It is common in marshy places throughout the Holarctic, extending southwards in Europe to northern Italy. Most of this range is probably occupied by the true *A. laevis*, showing only slight infra-specific variation. *A. laevis* has been widely introduced into tropical regions and oceanic islands, where it has been recorded under many different names. For example, specimens from Hawaii in the B.M. (N.H.) labelled as *A. bevenoti* Collinge (Kauai) appear to belong to the aphyllid form of this species, and others labelled as *A. perkinsi* Collinge (Lanai) and *A. globosus* Collinge (Mauna Loa) to the ephyllid form.

### *Fossil record*

Pleistocene to Recent.

### *Material examined*

Living specimens from many places in England and Wales. Spirit specimens from the type locality (Frederiksdal, Denmark), kindly collected and sent to me by Dr. Mandahl-Barth, and from Britain, South America, New Zealand and Hawaii.

### *Agriolimax caruanae* Pollonera, 1891

*Agriolimax caruanae* Pollonera, 1891 : 3. Porta Reale, Malta.

### *Notes*

Pollonera described the keel of his species as blackish, and figured a more globular spermatheca than is found in adult British specimens. However, in Britain the keel and head are the first parts to pigment, so that in young animals they are darker than the rest of the body. The spermatheca is sometimes globular, in young animals at any rate in Britain, and in adults of some American forms. Pilsbry (1948 : 558) figures considerable variation between American specimens, which he nevertheless recognizes as belonging to *A. caruanae*. The British slug can be at most a geographical race of this species, of which Quick (1949 : 28) gives a short account.



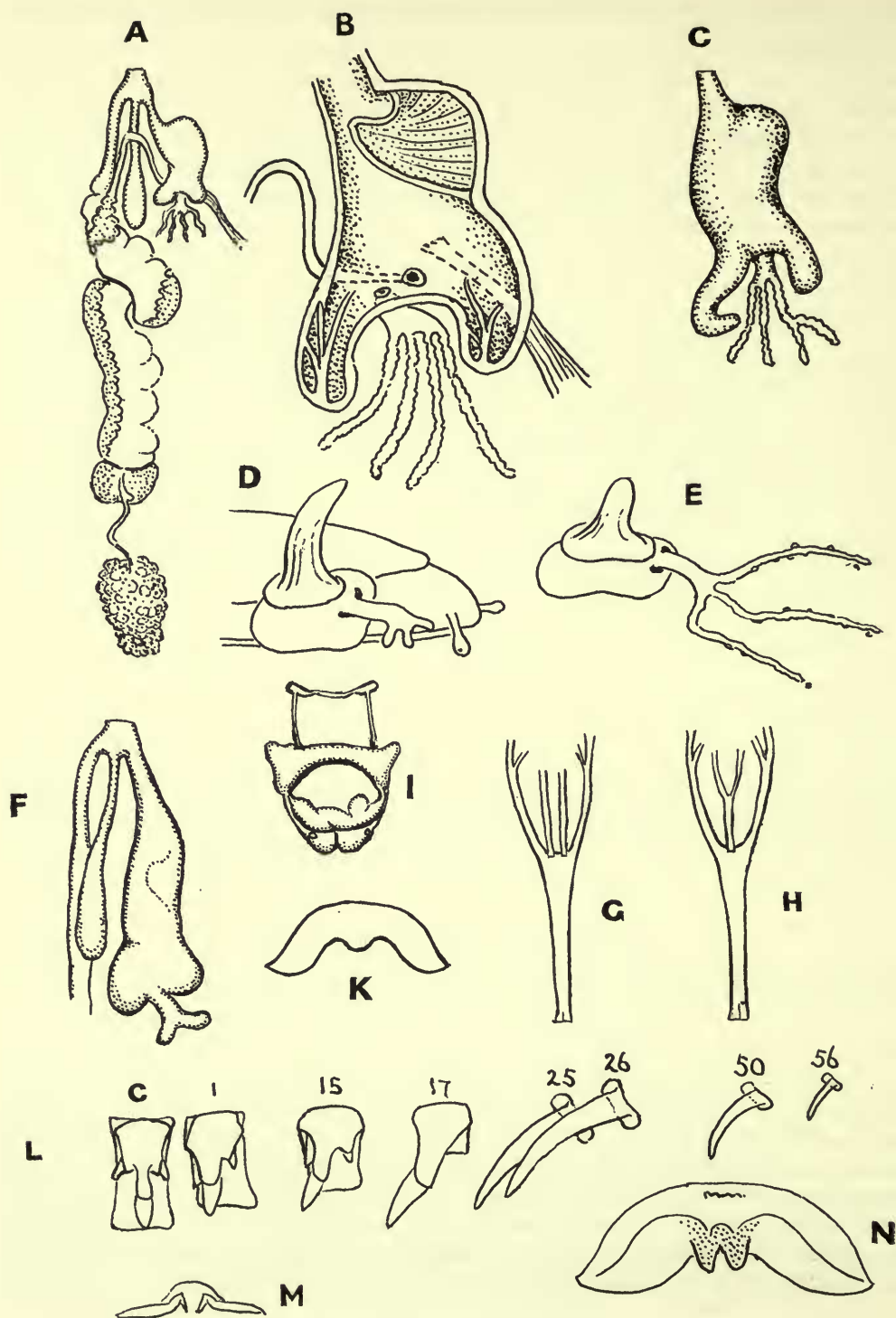


FIG. 12.



*First British record*

Specimens, found by the late Charles Oldham in Cornwall about 1930, were identified with this species (as perhaps a distinct subspecies or variety) by H. Watson, and exhibited at meetings of the Conchological Society of Great Britain and Ireland and the Malacological Society of London.

*Diagnostic features*

Distinguished in life from the externally similar *A. laevis* by larger size and even greater activity. Internally distinguished by having two penial diverticula and a tuft of appendages, a darkly-pigmented visceral cavity, and a greater number of marginal radular teeth.

*External appearance* (Pl. 2, fig. 17)

The length when extended is 2.5–3 cm, or a little more. As in *A. laevis*, the head and neck extend far beyond the mantle. The slug is dark translucent chestnut brown, greyish-brown or grey, with the mantle lighter over the pallial region, and the body and mantle more or less flecked with dark brown. The respiratory orifice is pale rimmed. The sole is grey rather than brown, because the dark visceral pigmentation shows through the tissues. The mucus is thin and colourless.

*External variation*

The colour varies from a clear chestnut-brown to a greyer brown, and the small darker flecks on body and mantle are more or less marked, but there are no named varieties.

*Shell* (Text-fig. 10 H)

4.5 × 2 mm, or a little larger. In undistorted specimens, the right border is slightly concave.

*Pallial organs* (Text-fig. 10 E)

As in *A. reticulatus*.

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FIG. 12. *Agriolimax caruanae*. A. Reproductive organs (× 4). B. Penis (× 14) opened to show sarcobelum, two diverticula, entries of vas deferens and crenulate branched appendix, penial retractor. C. Penis (× 8). D. Sarcobelum protruded, atrium everted, appendix beginning to be everted. E. Three branches of appendix fully everted, sarcobelum beginning to shrink. F. Distal genital ducts (× 30) of young individual 11 cm long, showing oviducts, spermatheca, sarcobelum in penis, rudiments of diverticula and appendix. G & H. Cephalic retractors. The buccal retractor is sometimes completely divided. I. Ganglia and commissures of nerve ring. K. Jaw (× 20). L. Representative radular teeth (× 500). M. Jaw (× 100) of individual one day old. N. Jaw (× 100) of young individual 6 mm long.

*Retractor muscles* (Text-figs. 12 G and H)

The cephalic retractors arise by a common stem, and the buccal retractor is divided either completely or for half its length.

*Nervous system* (Text-fig. 12 I)

As in *A. reticulatus*.

*Jaw* (Text-fig. 12 K)

Of the usual oxygnathous type, 1.3 mm across. In the newly-hatched animal, a median indentation (like that seen in *Milax*, *Limax* and *Vitrina*) reveals a bilateral origin (Text-figs. 12 M and N).

*Radula* (Text-fig. 12 L)

Characterized by having rather fewer lateral teeth and more marginals than *A. reticulatus* and *A. agrestis*. Formula C.14.55.

*Alimentary system* (Text-fig. 10 C)

As in *A. laevis*, there is no rectal caecum. The walls of the visceral cavity are darkly pigmented.

*Reproductive system* (Text-figs. 10 C and 12 A-F)

The dark ovotestis lies rather far forwards, and is partly exposed on the left side of the visceral mass. The oviduct, atrium and spermatheca require no special comment. The basal segment of the penis is slender and the segment containing the sarcobelum capacious. The distal segment bears apically two curved hollow processes, of which the left is often the longer, and between these an appendix with four or five long slender crenulated branches, corresponding with the apical appendix of *A. reticulatus*.

*Mating* (Text-fig. 10 K)

Breeding occurs throughout the year, eggs having been seen in January, May, June, July, October, November and December. A mating pair was observed on 25th June, 1950. At 6.10 p.m. the partners were following one another in a circle, with protruded sarcobela, licking one another's tails. At 6.40 they were lying quietly with their necks close together, with the atria everted and the sarcobela shrinking. A few seconds later, the four long tubular branches of the penial appendices were everted, lying across the partner's body like hyaline threads. At 6.42 the everted organs were rapidly withdrawn, with the sarcobela last, and the animals crawled apart.

Individuals from Glamorgan and Denbigh, isolated from birth, have on several occasions been seen to lay a few self-fertilized eggs, which have developed to an advanced stage although they have not been seen to hatch. Gregg (1944) reports fertile eggs from virgin specimens in California. There this species (for which Gregg

uses the name *Deroceras panormitanus*) apparently passes through a purely female phase when about half grown. Only about half the individuals survive this phase, to grow to full size and develop male organs. There is no sign of such a female phase in Britain, where slugs only 10 mm long, with their common ducts still slender and immature, always have penes in which the rudiments of all the adult features are easily recognizable. Two diverticula, a budding tufted appendix and a sarcobelum can be seen in a penis between 1.3 and 1.6 mm long. Aphallic and hemiphallid individuals are unknown in Britain. In any case, aphallic individuals of *A. laevis* are not in a female phase, since they have spermatozoa and a prostate. Gregg's observations are explicable in two ways: he may possibly have been working with a mixed culture of *A. caruanae* and *A. laevis*, or the difference may be related to the more rapid development of *A. caruanae* in California than in Britain.

#### *Development*

The eggs are relatively small, from  $1.5 \times 1.5$  to  $1.75 \times 1.4$  mm: much smaller than those of *A. reticulatus* and *A. agrestis*, and not much larger than those of *A. laevis*. They are laid in clusters of up to fifty eggs, and in the summer hatch in about seventeen days. The young are only about 3 mm long, very pale and translucent, with pale violet tentacles. Pigmentation begins at the head and tail, as in *A. laevis*.

#### *Behaviour*

*A. caruanae* crawls extraordinarily fast for a slug, and is irritable and pugnacious, snapping at its neighbours and lashing its tail. Even when well supplied with food, it shows cannibalistic tendencies.

#### *Ecology*

Usually confined to gardens, in flower and vegetable beds, lawns, rubbish heaps and greenhouses; but occasionally found at a distance from houses, in hedges, fields and waste places (records from Devon and Glamorgan).

#### *Distribution* (Map 18)

Recorded from scattered localities in England (mainly in the west), Wales, Scotland and southern Ireland (Makings, 1959). The extra-limital distribution is very imperfectly known. Repeated efforts to obtain topotypes from Malta have failed. The species probably occurs at Marseilles (Pilsbry, 1948: 560), and has been introduced into California.

#### *Fossil record*

Holocene shells from Romney Marsh (Hayward, 1954*a* and *b*) are very suggestive of this species. Although slug shells are badly characterized, especially when fossil, there is a *prima facie* case for believing that these are indeed shells of *A. caruanae*. Otherwise, the species is known only from Recent deposits.

#### *Material examined*

Living or spirit specimens from St. Agnes, Scilly Isles; Exeter, Devon; Swansea

and Porteynon, Glamorgan ; Old Colwyn, Denbighshire ; St. Albans, Hertfordshire ; Bromborough, Cheshire ; Edinburgh and Aberdeen, Scotland ; Cork (grounds of the University, from Dr. Makings) and Newcastle, Co. Down (Dr. Stelfox's garden), Ireland ; Pyrenées Orientales ; Golden Gate Park, San Francisco.

### Genus *LIMAX* Linnaeus, 1758

Type species *Limax maximus* Linnaeus, 1758.

Limacinae in which the right ocular retractor passes forwards between the penis and the vagina. The intestine has two forwardly-directed loops, and the left lobe of the liver forms the apex of the visceral mass. There is no penial stimulator. The nucleus of the concentric mantle ridges lies in the mid-dorsal line. The dorsal keel slopes evenly to the end of the tail, which is therefore pointed and not truncated.

Hesse (1926 : 8-16, 76-92) divides *Limax* into several subgenera, and the nominate subgenus into sections. Since no regular trends in several characters are discernible, each species being specialized in some respect or another (e.g. the long penis and peculiar mating behaviour of *L. maximus* and *L. cinereoniger*), the infrageneric arrangement depends largely on the relative systematic importance attached to the radula, penis, alimentary tract and other organs. For example, *L. nyctelius* may be associated with *L. flavus* in the section *Limacus*, on the basis of its rather long cylindrical penis and long rectal caecum ; but their radulae are very different, that of *L. flavus* being specialized in the suppression of ectocones and endocones, while that of *L. nyctelius* approaches the condition of *Agriolimax*. Subgeneric and sectional names are therefore not adopted here.

### *Limax tenellus* Müller, 1774

*Limax tenellus* Müller, 1774 : 11. Denmark.

*Limax tenellus*; Nilsson, 1822 : 11.

*Limax serotinus* Schrank, 1848 : 144.

*Limax cereus* Held, 1849 : 15.

*Limax fulvus* Normand, 1852 : 7.

*Agriolimax tenellus*; Lessona & Pollonera, 1882 : 45, pl. 1. fig. 7.

#### Notes

Although Nilsson is often quoted as the author of this name, it was first applied by Müller. Ignoring an obvious mistake in measurement, Müller's description seems adequate to identify the present species : "*Limax virescens*, capite tentaculisque nigris. Dan. SPÆD-SNEGLEN. long. 10 unc. Totus albidus, *Clypeus* in luteum, abdomen in virescentem colorem aliquantum vergit ; ille margine postico, hoc apice supra nigricat. In Fossulis Nemorum foliis aridis repletis ; primo vere."

Altena (1958) confirms that *L. fulvus* Normand is indeed *L. tenellus*.

#### First British record

By Alder (1848 : 124).



*Diagnostic features*

Distinguished externally from other British species by small size, and pale yellow colour, with black head and tentacles; and internally by a short penis with no appendix.

*External appearance* (Pl. 2, fig. 16)

The smallest British *Limax*, from 25 to 35 mm long when extended. Colour pale yellow, or sometimes reddish-brown, with blackish head and tentacles, and sometimes with a pair of more or less distinct body and mantle bands. The mucus is yellow.

*External variation*

Var. *cerea* Held (1849), uniform yellow, or with mere traces of bands; var. *fulva* Normand (1852), reddish-brown, suffused dorsally with black; var. *cincta* Heyne-mann (1861), with distinct dark mantle bands, and sometimes body bands.

*Shell*

Thin and delicate, measuring about  $3.5 \times 2$  mm.

*Pallial organs* (Text-fig. 13 D)

The somewhat angularly crescentic kidney partly embraces the heart and pericardium, just behind the origin of the penial retractor.

*Retractor muscles* (Text-fig. 13 E)

The cephalic retractor arises by two roots in the mid-dorsal line just behind the kidney, and divides about half-way along into right and left tentacular retractors. The right tentacular retractor passes forwards between the penis and oviduct, and not on the left of both as it does in *Milax* and *Agriolimax*. The pharyngeal retractor arises half-way along the left tentacular retractor, and divides into right and left branches passing to the buccal bulb between the cerebral and visceral ganglia. The penial retractor arises from the diaphragm on the left side, in front of the pericardium.

*Nervous system* (Text-fig. 13 H)

The olfactory and optic lobe of the cerebral ganglion is large, the cerebro-pleural and cerebro-pedal commissures short, and the visceral ganglia closely approximated, the right visceral and abdominal ganglia being fused together.

*Jaw* (Text-fig. 13 F)

Of the usual oxygnathous type, 1.5 mm across.

*Radula* (Text-fig. 13 G)

The central tooth,  $0.038 \times 0.018$  mm, with small but distinct ectocones, is flanked on each side by about twenty lateral teeth with both ectocones and endocones,



followed by about forty-five marginal teeth. The teeth between the eighteenth and twenty-second are transitional in character, the endocone diminishing, and the ectocone approaching the mesocone. In the marginals, the mesocone becomes relatively longer and more curved, and the ectocone becomes prominent, arising from the side of the mesocone. Ectocones occur in some of the outer marginals of other *Limax* species, but they are not the conspicuous feature throughout that they are in *L. tenellus*. Formula C.20.45  $\times$  110.

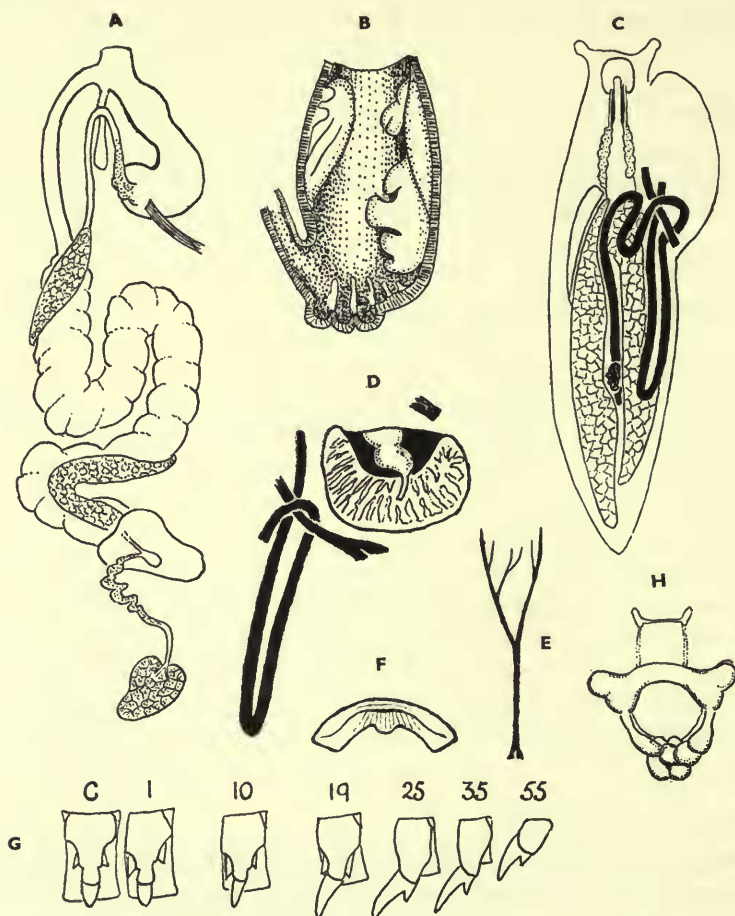


FIG. 13. *Limax tenellus*. A. Reproductive organs ( $\times 4$ ). B. Penis ( $\times 6.7$ ) opened. C. Alimentary system, showing left lobe of liver forming apex of visceral mass, ovotestis at stomach level, between left and right lobes, intestine, cephalic retractor, oesophagus, salivary glands, buccal bulb, portion of albumen gland below left liver lobe. D. Kidney, heart and pericardium, origin of penial retractor in front, second forwardly-directed loop of intestine passing around cephalic retractor, rectum. E. Cephalic retractor muscles. F. Jaw ( $\times 14$ ). G. Representative radular teeth ( $\times 330$ ). H. Nerve ganglia ( $\times 8$ ).

*Alimentary system* (Text-fig. 13 C)

The left lobe of the liver forms the apex of the visceral mass. The apex of the stomach forms the most posterior part of the alimentary tract (which in *Limax* has almost lost the spiral torsion seen in *Arion* and in *Milax*), and the intestine has two forwardly directed loops. The first of these is held in place by the aorta as usual, and the second, which extends further forwards, is crossed by the cephalic retractor. The intestine runs backwards from this point and turns sharply to run forwards as the rectum, between the cephalic retractor and the floor of the pulmonary chamber, to the posterior lip of the respiratory orifice.

*Reproductive system* (Text-fig. 13 A)

The darkly pigmented ovotestis lies behind the stomach, but a little of it may be visible from the dorsal aspect, between the right and left lobes of the liver. The dilated central part of the hermaphrodite duct is pigmented and sinuous, narrowing at the albumen gland, where it has a distinct unpigmented vesicula seminalis. The prostate does not diverge anteriorly from the oviduct. The short vas deferens, which is not bound down by the right ocular retractor, becomes sacculate and pigmented at the entrance to the penis, apically above the insertion of the penial retractor. Internally the penis (Text-fig. 13 B) shows three or four delicate short transverse folds apically, and further forwards three main massive longitudinal folds, the exact appearance varying according to where the penis is opened. These folds are visible during copulation (see below). The spermatheca is small and club-shaped, with a short duct entering the atrium.

*Mating*

According to Gerhardt (1933 : 445), one animal follows the other rapidly, head to tail. The leader soon bends to the right, so that after ten minutes the circle is completed. The penes are suddenly everted as massive bluish-white bodies, each with a thickened oblique fold which Gerhardt calls the comb. The penes are closely apposed, but not entwined, and the animals slowly revolve clockwise for one and a half hours. *L. tenellus* differs from *L. maximus* and *L. cinereoniger* in not entwining the body nor hanging from a horizontal surface.

*Development*

The eggs vary from  $3.6 \times 3.1$  to  $3.3 \times 3.0$  mm, and are pale amber, soft, translucent and slightly adherent. In Britain, they are laid from November to March in clusters of about fifteen, and take from sixty to 120 days to hatch. The young are 6 mm long, with a slight dorsal keel posteriorly. They are white and translucent, without body and mantle bands and with a more opaque kidney region. The tentacles are pale violet, with the dark brown retractor muscle showing through.

*Ecology*

Restricted to woodlands, usually of considerable extent, and one of the few slugs found in pine woods. Absent from most of the many woods and plantations

established during the seventeenth century, which suggests that its powers of dispersal are poor. Indifferent to the presence or absence of lime.

### *Distribution* (Map 19)

Of very local occurrence, though wide range, and therefore seldom encountered. In Britain, recorded from many vice-counties. In Europe, found from France northwards to Jemtland, and eastwards to the Caucasus.

### *Material examined*

Living specimens from Netley Heath, Shere, Surrey ; and Chepstow, Monmouthshire. Spirit specimens from Britain and Switzerland.

## *Limax flavus* Linnaeus, 1758

*Limax flavus* Linnaeus, 1758 : 652. Sweden.

*Limax variegatus* Draparnaud, 1801 : 103.

*Limax megalodontes* Quoy & Gaimard, 1824 : 426.

### *First British record*

By Lister (1685-97, pl. 101*b*).

### *Diagnostic features*

Tentacles steely blue, body and mantle with yellowish spots and no lateral bands. Long rectal caecum and long cylindrical penis—a diagnostic combination for British *Limax*.

### *External appearance* (Pl. 2, fig. 22)

A rather large slug, from 7 to 10 cm long when extended. Colour from yellowish to greenish, more or less suffused with dusky pigment, and mottled on the mantle with yellow patches, on the body with yellow spots formed by groups of up to seven tubercles. There are no lateral bands. The tentacles are a very characteristic cold steely blue, the sole pale yellow, the respiratory orifice pale-rimmed, and the mucus yellow.

### *External variation*

Var. *rufescens* Moquin-Tandon (1855), reddish-brown ; var. *virescens* Férussac (1819), uniformly greenish ; var. *antiquorum* Sowerby (1834 ?), pale ochraceous marbled with grey ; var. *breckworthiana* Lehmann (1864), uniformly suffused with dark pigment.

### *Shell*

Rather large, 9 × 6 mm, thin and convex, with the nucleus near the posterior margin and a little to the left of the mid-line.

*Pallial organs*

As in *L. tenellus*.

*Retractor muscles* (Text-fig. 14 D)

The cephalic retractors arise from two roots, which do not unite for a considerable distance. The buccal retractor arises near the origin of the left ocular retractor. The penial retractor arises from the diaphragm, in the region of the kidney.

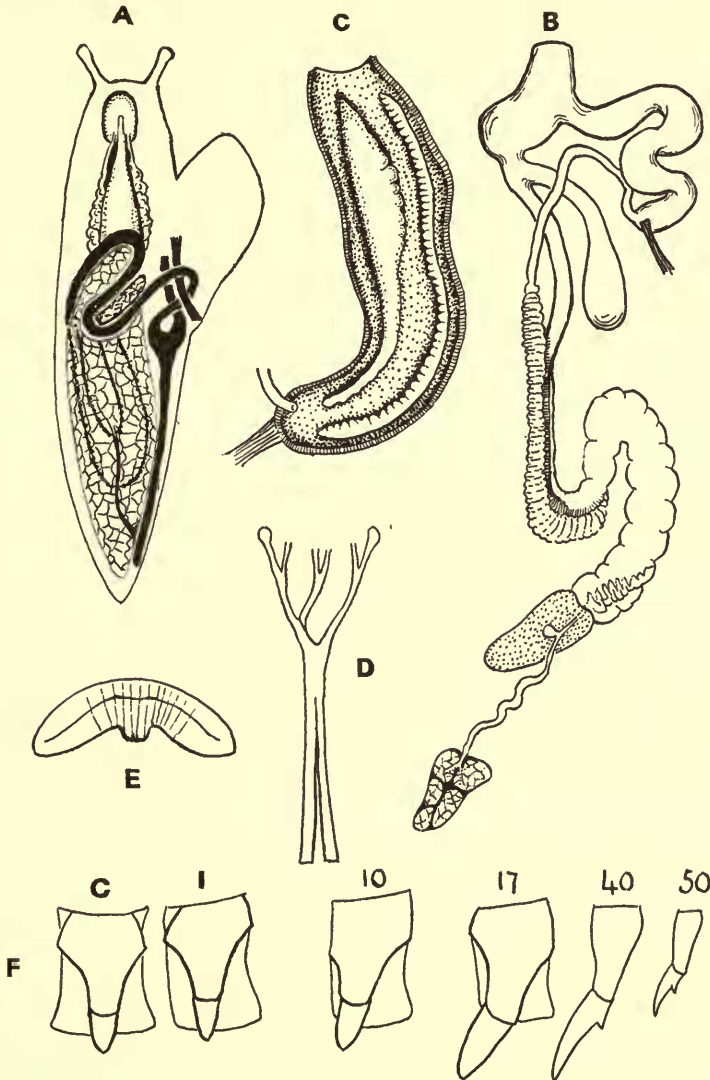


FIG. 14. *Limax flavus*. A. Alimentary system ( $\times 2$ ) showing second forwardly-directed loop of intestine passing around cephalic retractor, long rectal diverticulum passing backwards. B. Reproductive organs ( $\times 2$ ). C. Penis ( $\times 6$ ) opened to show internal folds. D. Cephalic retractor muscles. E. Jaw ( $\times 14$ ). F. Representative radular teeth ( $\times 330$ ).



*Nervous system*

As in *L. tenellus*.

*Jaw* (Text-fig. 14 E)

2.25 mm across, dark brown in colour. Marked transversely with fine striae, which are crossed by still finer ones following the contour of the jaw.

*Radula* (Text-fig. 14 F)

Measures  $6.5 \times 2.6$  mm, with about 150 rows of teeth. The central tooth (measuring  $0.05 \times 0.038$  mm) has a strong mesocone, but its ectocones are obsolete or absent. The lateral teeth are also devoid of ectocones and endocones. The aculeate marginals, some of the outermost of which have small ectocones, are connected to the laterals by several transitional teeth. Formula  $C.16+4.50 \times 150$ .

*Alimentary system* (Text-fig. 14 A)

The oesophagus dilates to a capacious crop, flanked by the salivary glands, and merging gradually into the stomach. The second forwardly directed loop of intestine is held in place by the cephalic retractor muscle. Instead of being prolonged backwards as it is in *L. tenellus*, it soon turns forwards as the rectum; but from the apex of the bend a long rectal diverticulum extends backwards, on the surface of the liver, to the end of the body. As in the other species of *Limax*, the left liver lobe forms the apex of the visceral mass.

*Reproductive system* (Text-fig. 14 B)

The unpigmented ovotestis lies between the lobes of the liver, well below the stomach apex. The hermaphrodite duct, at its entrance to the yellow linguiform albumen gland, has a rounded white seminal vesicle. The ribbon-like yellow prostate diverges from the oviduct anteriorly, and can easily be peeled off it for the greater part of its length. The vas deferens runs forward, and turns back beneath the right ocular retractor to the apex of the penis. The penis is a rather long cylindrical organ, strongly folded in a spiral. Internally it bears (besides three or four minor longitudinal folds) a long, low, crinkled, ribbon-like fold along its whole length, and another more prominent fold that expands distally to a crest or "comb", lobulated or crenulated on the free margin (Text-fig. 14 C). The oviduct expands at its entrance to the atrium, where the spermatheca arises from it.

*Mating*

Mating occurs from late summer to February. According to Gerhardt (1933), after "following" for about eight minutes, the animals approximate the right sides, but do not curve into a circle. The penes are rapidly everted and entwine spirally, forming a mass of about one square centimetre in area. Sperms enclosed in a mucous mass are transferred between the penes, which are rapidly withdrawn carrying the partner's sperms with them. The whole process occupies only half



a minute. Gerhardt does not state what follows, but presumably the sperms are transferred from the withdrawn penes to the spermathecae.

### *Development*

The eggs are laid in clusters of up to twenty, and have been found in September and February. They are large,  $6 \times 4$  mm, pale amber in colour, and differ from those of other British slugs in having a small rounded projection at each end, so that they resemble miniature lemons. They hatch in from three to six weeks at room temperatures. The newly-hatched young are from 10 to 13 mm long, pale greenish-yellow with the characteristic blue tentacles already evident. There are no bands at any stage, and the yellow spots of the adult appear later in development.

### *Behaviour*

*L. flavus* is essentially nocturnal, and unless looked for after dark it may escape observation in urban surroundings, even where it is abundant.

### *Ecology*

*L. flavus* is found in woods, under logs and bark, but is much commoner in gardens, in the crevices of walls, and in cellars and out-houses. It eats decaying vegetable matter, fungi and lichens in wild places, and mildew and garbage in gardens and out-houses.

### *Distribution* (Map 20)

Probably occurs in every vice-county of the British Isles, and ranges from southern Norway to North Africa and eastwards to Syria. It has been introduced into South Africa, Australia and North and South America, and to islands in the Atlantic and Pacific.

### *Material examined*

Living specimens from Swansea, Glamorgan; and Reading, Berkshire. Spirit specimens from Britain, Corsica, Greece, North and South America, South Africa, Australia, and the New Hebrides and Cook Islands.

## *Limax cinereoniger* Wolf, 1803

*Limax cinereoniger* Wolf, 1803 : 7. Germany.

*Limax antiquorum* Férussac, 1819 : 68 (in part).

*Limax maximus*; Gray, 1840 : 113 (in part).

*Arion lineatus* Dumont, 1850 : 64.

*Limax cinereus* var. *intermedia* Brevière, 1881 : 314.

### *First British record*

By Gray (1840).

*Diagnostic features*

Largest British slug, usually black with dorsal line and median zone of sole white, keel prominent and rather long. Distinguished from *L. maximus* by coloration, and by coarser tubercles, spotted tentacles, relatively small shell and jaw, and longer penis not tapering distally.

*External appearance* (Pl. 2, fig. 25)

This is our largest native slug, which grows to 10 or 20 cm long in this country, while some continental forms are even larger. The keel is prominent and long, and the tubercles relatively coarser than in *L. maximus*. The slug is usually black all over, except for the white mid-dorsal line and median area of the sole. The dark tentacles are spotted with small discrete black or dark brown dots—a character distinguishing the species from *L. maximus*, which has apparently not been recorded previously.

*External variation*

In Britain the ground colour, seen in the mid-line and the median area of the sole, is usually whitish, but in continental specimens the keel may be red or yellow. The following named varieties have been recorded from Britain: var. *ornata* Lessona (1880), body black with a series of white spots along each side; var. *maura* Held (1836), entirely black; var. *cinerea* Moquin-Tandon (1855), entirely ash-coloured except for bluish-black mantle; var. *punctata* Lessona (1880), keel and mid-line of dorsum yellow, two interrupted bands on each side.

*Shell*

Relatively smaller (9 × 5 mm), thinner and slightly more elongated than that of *L. maximus*.

*Pallial organs*

As in *L. tenellus*.

*Retractor muscles*

The slender cephalic retractor arises from the mid-line behind the diaphragm, and crosses the second forwardly-directed intestinal loop. The right ocular retractor passes (as is usual in *Limax*) between the male and female divisions of the distal genital ducts, over the vas deferens. The penial retractor arises broadly from immediately to the left of the cephalic retractor, and narrows to its insertion at the apex of the penis.

*Nervous system*

As in *L. tenellus*.

*Jaw* (Text-fig. 15 E)

Usually about 3 mm across, but may reach 4 mm in very large specimens : relatively smaller than in *L. maximus*.

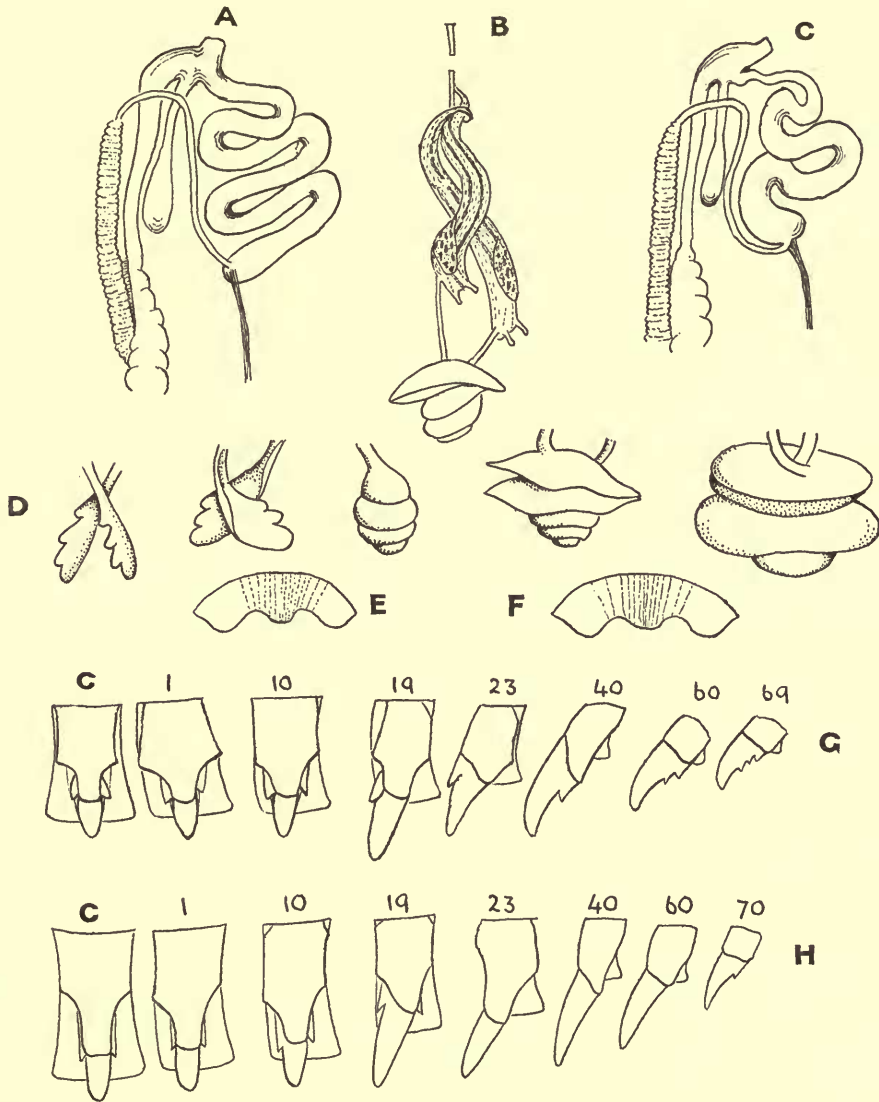


FIG. 15. *Limax*. A. *L. cinereoniger*—distal genital ducts ( $\times 1.3$ ). B. *L. maximus*—mating pair suspended from mucus thread (adapted from L. Adams). C. *L. maximus*—distal genital ducts ( $\times 2$ ). D. *L. maximus*—stages in eversion and entwining of penes (adapted from L. Adams). E. *L. cinereoniger*—jaw ( $\times 6.7$ ). F. *L. maximus*—jaw ( $\times 6.7$ ). G. *L. cinereoniger*—representative radular teeth ( $\times 330$ ). H. *L. maximus*—representative radular teeth ( $\times 330$ ).

*Radula* (Text-fig. 15 G)

There are about 150 rows of teeth. The central tooth has rather small but strong ectocones. It is flanked by about nineteen laterals, with ectocones and endocones, the latter descending on the mesocones in the outer teeth. There are about fifty marginals on each side, of which only the inner teeth retain the endocone. In the outer marginals, an ectocone appears on the concave side of the mesocone, and becomes bifid or trifid in a few of the outermost teeth. Formula C.19.50  $\times$  150.

*Alimentary system*

Resembles *L. tenellus*, and differs from *L. flavus*, in having the loop of intestine which is retained by the cephalic retractor prolonged backwards almost to the visceral apex, and without a rectal caecum. The loop is longer than in *L. maximus*.

*Reproductive system* (Text-fig. 15 A)

The long narrow darkly pigmented ovotestis is visible on the surface between the left and right liver lobes. The hermaphrodite duct is pale, slender at first, then wider and folded, and narrows at the somewhat triangular albumen gland. If a seminal vesicle is present, it is small, deep in the albumen gland and difficult to find. The folded common duct narrows to a long free oviduct, dilated at its entry into the atrium, and the small club-shaped spermatheca arises one or two millimetres before its end. The prostate separates from the common duct and so is free at its anterior end, and the vas deferens passes under the right ocular retractor and back to the apex of the penis. The stout cylindrical contorted penis is of nearly uniform diameter throughout its length, and when straightened out is from 6–8 cm long. Internally it bears a prominent fold, double at its origin. In its upper part this expands into a prominent frill, the "comb". The rest of the mucous membrane is circularly ridged.

*Mating*

Mating occurs at night, throughout the milder periods of the year, on vertical or overhanging surfaces. After about fifteen minutes of "following", the animals hang down freely from a disk of mucus. Their bodies and the evaginated penes, which become as long as the bodies, are entwined. A mass of sperms enclosed in mucus descends each vas deferens inside the penis, and the sperm packets are exchanged between the "combs" which are now terminal. The penes are then withdrawn, carrying the sperms with them to be transferred later to the spermathecae. The whole process takes about twenty minutes.

Auto-fecundation can occur in this species (Oldham, 1942a).

*Development*

The eggs are about 5  $\times$  5.5 mm, soft, translucent and amber-coloured. On account of the large size of the eggs, and their transparency when under water, the caudal and cephalic vesicles of the embryos can easily be observed (Text-fig. 18 H). The

eggs hatch in about a month. The newly hatched young are translucent white, but soon become opaque, then brown and finally black. There is sometimes a suggestion of banding, and the lateral areas of the foot are the last to pigment.

Oldham (1942a) records that this slug becomes mature in two years, and that an individual in captivity lived for five years and 270 days.

### *Ecology*

This is essentially a slug of wild places, being found beneath logs and leaves and in tree crevices of ancient woodlands. In Pembrokeshire at least, it also occurs on damp lichen-covered rocks on bare hillsides. It seems never to occur in gardens and cultivated land or recent plantations. Though in the wild it presumably feeds on lichens, fungi and decaying vegetable matter, in captivity it readily eats carrot, oatmeal etc.

### *Distribution* (Map 21)

*L. cinereoniger* is recorded from most British vice-counties, except for East Anglia and parts of central England, southern Scotland and central Ireland. In Europe, it extends from arctic Norway to north-eastern Spain, Italy, Sardinia, Greece and the Crimea.

### *Material examined*

Living specimens from Netley Heath, Surrey ; Cusop Dingle, Hereford ; Bucklebury, Berkshire ; and Pont Neath Vaughan, Glamorgan. Spirit material from Britain, Denmark, Germany and Luxemburg.

## *Limax maximus* Linnaeus, 1758

*Limax maximus* Linnaeus, 1758 : 652. Sweden.

*Limax cinereus* Müller, 1774 : 5.

*Limax antiquorum* Férussac, 1819 : 68 (in part).

### *First British record*

By Lister (1674 : 99).

### *Diagnostic features*

Large, differs from *L. cinereoniger* in coloration : grey or brown with two or three bands on each side of body, dark spotting or marbling on mantle, tentacles pale pinkish-brown without spots, sole uniformly pale ; and also in having the tubercles relatively smaller, the shell and jaw relatively larger and the penis shorter and tapering distally.

### *External appearance* (Pl. 2, fig. 24)

Length from 10 to 20 cm. The tubercles are relatively smaller than in *L. cinereoniger*. The slug is usually some shade of grey, with a uniformly pale sole.



The body bears two or three bands, often doubled or more or less interrupted, on each side. The mantle is irregularly spotted or marbled with dark pigment, but never banded. The tentacles are translucent pinkish-brown, without spots.

### *External variation*

The ground colour may be grey, ochraceous or reddish, and the bands may be developed to an infinitely variable degree. Named varieties are: var. *concolor* Pini (1876), uniformly ash-coloured; var. *candida* Lessona & Pollonera (1882), white, translucent, eyes pale brown; var. *vinosa* Baudon (1884), purple or vinous brown; var. *fasciata* Razoumowsky (1789), ash-coloured with three bands on each side; var. *sylvatica* Morelet (1845), ash-coloured with two bands, and an indistinct third lower band; var. *tetrazona* Taylor (1902), with only two bands on each side; var. *cellaria* Dezallier d'Argenville (1742), bands interrupted; var. *aldrovandi* Moquin-Tandon (1855), ash-coloured with pale spots; var. *tigris* Taylor (1902, from Adams MS.), tawny yellow with black bands.

### *Shell*

Measures about  $11 \times 7$  mm, and is thus relatively larger than that of *L. cinereoniger*.

### *Pallial organs, retractor muscles, nervous system*

As in *L. cinereoniger*.

### *Jaw* (Text-fig. 15 F)

Relatively larger (3.5 mm across) than that of *L. cinereoniger*.

### *Radula* (Text-fig. 15 H)

The central tooth is larger and relatively narrower than in *L. cinereoniger*, and its ectocones are more delicate and sometimes almost obsolete. There are about nineteen lateral teeth on each side, all or most of which retain both ectocones and endocones. The marginals (about fifty on each side) lack endocones, and only some of the outermost teeth have small ectocones. Formula C.19.50.

### *Alimentary system*

As in *L. cinereoniger*, except that the last posteriorly-directed loop of intestine is shorter, reaching only about half-way along the visceral mass. There is no rectal caecum.

### *Reproductive system* (Text-fig. 15 C)

The ovotestis is of the same long flattened linguiform shape as in *L. cinereoniger*, but is pale or only slightly pigmented. The hermaphrodite duct, albumen gland, common duct, free oviduct and spermatheca are also similar. The distal end of the prostate diverges more or less from the oviduct, and above this the prostate is

only weakly attached for a considerable distance. The penis differs from that of *L. cinereoniger* in being shorter, widest apically and tapering distally. Internally there is a fold, expanded proximally into a "comb", as in *L. cinereoniger*.

#### *Mating* (Text-figs. 15 B and D)

This occurs at night from overhanging surfaces. Unlike *L. cinereoniger*, *L. maximus* hangs suspended in mid-air from a stout thread of mucus. The protrusion of the organs, sperm transfer, and withdrawal of the penes is as in *L. cinereoniger*, but the entwined penes are not so long. After withdrawal, the animals re-ascend the mucus thread. Adams (1898) gives further details.

#### *Development*

The eggs,  $5.0 \times 5.5$  mm, resemble those of *L. cinereoniger*. They are laid in early spring and in the autumn. February eggs in an unheated room hatch in six and a half weeks. The young are pale grey, with the middle lateral bands visible from hatching—thus differing from young *Lehmannia marginata*, in which the upper band appears first and mantle bands are also present. The tentacles are pale pinkish-grey. After two or three weeks, the other body bands have appeared and begin breaking up, and the mantle becomes marbled.

*L. maximus* lives for at least three or four years.

#### *Ecology*

*L. maximus* occurs in woods, hedgerows and waste places, where it is sometimes found together with *L. cinereoniger*; but unlike the latter it occurs also in gardens, cellars and out-houses. It seems to avoid green leaves and to feed on fungi and decaying matter, though in captivity it readily eats oatmeal, Bemax etc.

#### *Distribution* (Map 22)

Apparently general in the British Isles, and found from Oslo and Petrograd to Asia Minor, Algeria and the Atlantic isles. Introduced into North America, South Africa, Australia, Tasmania and New Zealand.

#### *Material examined*

Living specimens from Swansea, Glamorgan; Savernake Forest, Wiltshire; Bucklebury Common, Berkshire. Spirit material from Britain, France, Greece, Azores, Madeira, Canary Isles and British Columbia.

### Genus **LEHMANNIA** Heynemann, 1861

Type species *Limax marginatus* Müller, 1774.

The penis is short, with a laterally-placed apical appendix (conical in *L. marginata*, short and cylindrical in *L. poirieri*, and long and cylindrical in *L. melitensis* Lessona & Pollonera). A long rectal caecum extends to the apex of the visceral mass. In

*L. poirieri* and *L. melitensis* the radula is like that of *Agriolimax*; but that of *L. marginata* is highly specialized. The body readily absorbs water and becomes swollen and translucent.

Hesse (1926) adopts sectional names within *Lehmannia*, segregating *L. marginata* (*Lehmannia* s.s.) from *L. poirieri* and *L. melitensis* (*Ambigolimax*) because of the former's specialized radula, although their reproductive and alimentary systems are very similar. As for *Limax*, subdivision of the genus depends on the importance ascribed to different characters.

### ***Lehmannia marginata* (Müller, 1774)**

*Limax marginatus* Müller, 1774 : 10. Denmark.

*Limax arborum* Bouchard-Chantreaux, 1837 : 164.

#### *First British record*

By the Reverend B. J. Clarke (in Thompson, 1840 : 204).

#### *Diagnostic features*

Gelatinous aspect in damp weather, mantle bands forming lyre-shaped figure, two body bands on each side; conical penial appendix, rectal caecum, specialized radula.

#### *External appearance* (Pl. 2, figs. 18 and 21)

Usually about 7.5 cm long, or larger. Its great capacity for absorbing water makes this slug become semi-transparent and gelatinous in appearance during damp weather. When irritated, it exudes copious watery mucus. In colour it is characteristically grey with a pale sole, two darker body bands on each side (which may be more or less indistinct or interrupted), and a pair of mantle bands forming an elongated lyre-shaped figure. The keel is paler than the body, and the median area of the mantle often darker.

#### *External variation*

Var. *glauca* Clarke (1843), ground colour greenish-grey; var. *subrufa* Le Compte (1871), ground colour yellow; var. *rosea* Broeck (1870), ground colour pinkish; var. *bettonii* Sordelli (1870), body bands fused together and interrupted; var. *tigrina* Wienland (1876), with rows of black spots on body and mantle; var. *rupicola* Lessona & Pollonera (1882), darkly pigmented, with indistinct markings.

#### *Shell*

White and iridescent. Normally measures  $4 \times 2.75$  mm, but varies considerably in size and thickness.

#### *Pallial organs*

As in *Limax*.

*Retractor muscles* (Text-fig. 16 c)

The main stem of the cephalic retractors arises from the mid-dorsal line just behind the kidney, and divides about half-way into the right and left ocular retractors. The buccal retractor arises from the left ocular retractor, a short distance in front of the bifurcation. The strong penial retractor arises from the diaphragm between the pericardium and the posterior border of the kidney, to be inserted below the vas deferens.

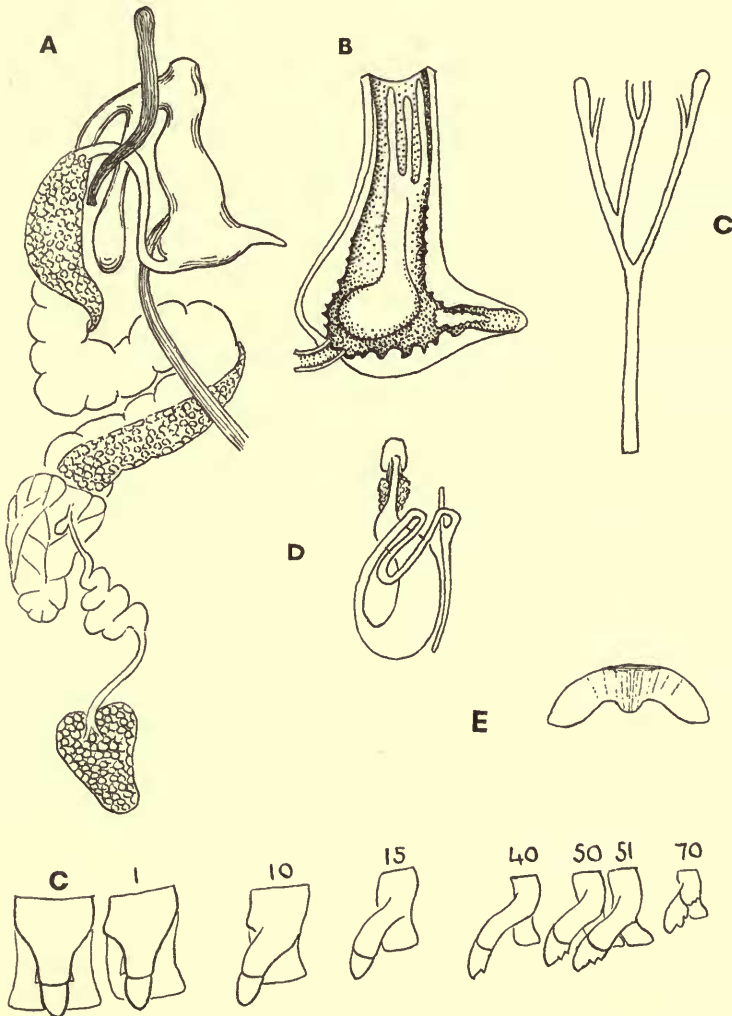


FIG. 16. *Lehmannia marginata*. A. Reproductive organs ( $\times 3.3$ ). B. Penis ( $\times 5.3$ ) opened longitudinally. C. Cephalic retractor muscles. D. Alimentary tract and salivary glands. E. Jaw ( $\times 13$ ). F. Representative radular teeth ( $\times 330$ ).



*Nervous system*

As in *Limax*.

*Jaw* (Text-fig. 7 E)

1.4 mm across, pale yellow in colour, and of the usual Limacid shape, not as narrow as figured by Taylor (1902-07, fig. 106).

*Radula* (Text-fig. 16 F)

Very characteristic, and easily distinguishable from the radulae of other British slugs. The central tooth has a strong, broad and short mesocone, and very small or obsolescent ectocones. It is flanked by ten or eleven laterals, with short wide mesocones and no ectocones, of which only the innermost one or two may have small endocones. The numerous marginals (up to seventy on each side) have characteristically strong, arched reflections bearing the short wide mesocones. From about the fortieth marginal outwards, the mesocone becomes bifid and then trifid, and minute denticulations corresponding to ectocones appear on the reflection.

*Alimentary system* (Text-fig. 16 D)

Resembles that of *Limax flavus*, with a rectal caecum extending backwards on the surface of the liver to the level of the stomach apex. The visceral cavity is darkly pigmented.

*Reproductive system* (Text-fig. 16 A)

The ovotestis is bulky and compact and superficially pigmented. The hermaphrodite duct is pale, swollen and folded in its median portion, and bears a rounded seminal vesicle where it terminates at the short linguiform albumen gland. The oviduct and spermatheca resemble those of *Limax*. The prostate is extraordinarily massive and deeply pigmented. The vas deferens, bound down by the right ocular retractor muscle, is short and wide, and enters the penis at the side of its blunt apex. At the opposite side of the apex there is a short conical appendix. The penis opened longitudinally (Text-fig. 16 B) shows a prominent fold, expanded and free at the apex and almost smooth, but corresponding with the "comb" of *Limax*. There is a small conical fold at the entrance to the appendix. The walls of the proximal part of the penis are thick and rugose.

*Mating*

This species can mate on level, vertical or overhanging surfaces.

*Development*

In Britain, mating occurs during the winter months. December eggs in an unheated room hatch in February. The eggs are soft, very translucent and pale amber in colour. They usually measure  $4.3 \times 3.6$  mm, but some are smaller. The young are 10 mm long, pale translucent grey with violet tentacles. They show well-marked



lyriform mantle bands, and a distinct band high up on the body—in contrast to young *Limax maximus*, in which the middle band is the first to appear.

### *Behaviour*

Like many (perhaps most) slugs, especially when young, *L. marginata* is able to suspend itself from a mucus thread secreted by the pedal gland. This thread passes back along the foot to the tip of the tail and adheres to a branch or other object, and supports the animal when it crawls off. Sometimes the slug can even turn around and re-ascend the thread. Kew (1902) gives numerous examples of this process, with details and some figures.

### *Ecology*

Not uncommon in old and newer woodlands, especially in the west and north. In dry weather it retreats into crevices in the bark and between roots, while in damp weather it crawls up the trunks to a height of twelve feet or more. It is also found on damp rocks on exposed hillsides, and on old stone walls.

### *Distribution* (Map 23)

Probably occurs in every vice-county of the British Isles, but is commoner in the west and north. In Europe it is found from Iceland and Lapland to Russia and Italy, and is recorded as introduced into Australia and New Zealand. In North America, it apparently occurs wild at Torbay, Newfoundland (confirmed by Altena, 1950). However, introduced slugs from Verdugo Woodlands, Glendale, California, kindly sent by Dr. W. O. Gregg and recorded as this species, proved to be *L. poirieri*. Probably some of the records from southern Europe also refer to *L. poirieri*.

### *Material examined*

Living specimens from the Gower Peninsula and the neighbourhood of Swansea, Glamorgan; Brecknock; Caernarvon; and Torrington, Devon. Spirit material from Britain and Australia.

## GREENHOUSE ALIENS

### *Lehmannia poirieri* (Mabille, 1883)

? *Limax valentianus* Férussac, 1823, 2 : 96<sup>e</sup>.

*Limax poirieri* Mabille, 1883 : 52. Spain.

### *Notes*

A full list of references is given by Altena (1950 : 9–17).

### *First British record*

By Quick (1949 : 24), as *L. valentianus*. However, Dr. A. D. J. Meeuse had already found it in a greenhouse in Belfast Botanical Gardens, on 26th November, 1948.

*Diagnostic features*

Somewhat like *L. marginata*, but the ground colour is yellower and paler, and the body bands nearer to the mid-dorsal line. The radula is like that of *Agriolimax*, very different from the specialized radula of *L. marginata*. The penial appendix is longer and more cylindrical than that of *L. marginata*, and not pointed at the apex.

*External appearance* (Pl. 1, fig. 14)

*L. poirieri* is about 6 cm long, with a yellowish-grey body and mantle, and slightly darker head. The general appearance is watery and translucent, like a pale *L. marginata*. The keel is short and inconspicuous. A pair of body bands, high up near the mid-dorsal line, are usually more or less interrupted and with scalloped outer edges. Sometimes faint traces of a second pair of bands occur lower down. A pair of mantle bands, becoming broader and darker behind, form a lyre-shaped figure, and the area enclosed is often darker in the centre and mottled with brown. The respiratory orifice is pale bordered. The tripartite sole is uniformly pale.

*External variation*

The mantle and body bands vary in width, completeness and the degree of crenulation of their outer borders, and there are sometimes faint traces of a second pair of body bands.

*Jaw*

Pale yellow, 2.25 mm across.

*Radula* (Text-fig. 17 D)

Like that of *Agriolimax* in having a distinctly tricuspid central tooth, and endocones on the lateral teeth—a feature which led Pollonera (1887a: 2) to place the species erroneously in that genus. The tri-cuspid central tooth is flanked by fifty-five to sixty teeth on each side, of which about fifteen are typical laterals with endo- and ectocones. Most of the inner marginals are simply aculeate, but many of the outer ones are bifid, while in the extreme outer ones the main cusp becomes multi-denticulate.

*Alimentary system*

The intestine shows the two forwardly-directed loops and the long rectal caecum reaching to the apex of the visceral mass, as in *L. marginata* and *Limax flavus*.

*Reproductive system* (Text-fig. 17 A)

Similar to that of *L. marginata*, but with the penial appendix longer, and bluntly cylindrical rather than conical. Pollonera (1887a) figures the appendix of *valentianus* as dilated and terminally vesicular, but this may result from misinterpretation of a somewhat folded appendix (Simroth, 1887). Altena (1950) found that Canadian

specimens had simple cylindrical appendices, like those of specimens from Swansea. Another difference from *L. marginata* is that the sac into which the spermatheca duct expands is somewhat sausage-shaped, rather than pyriform.

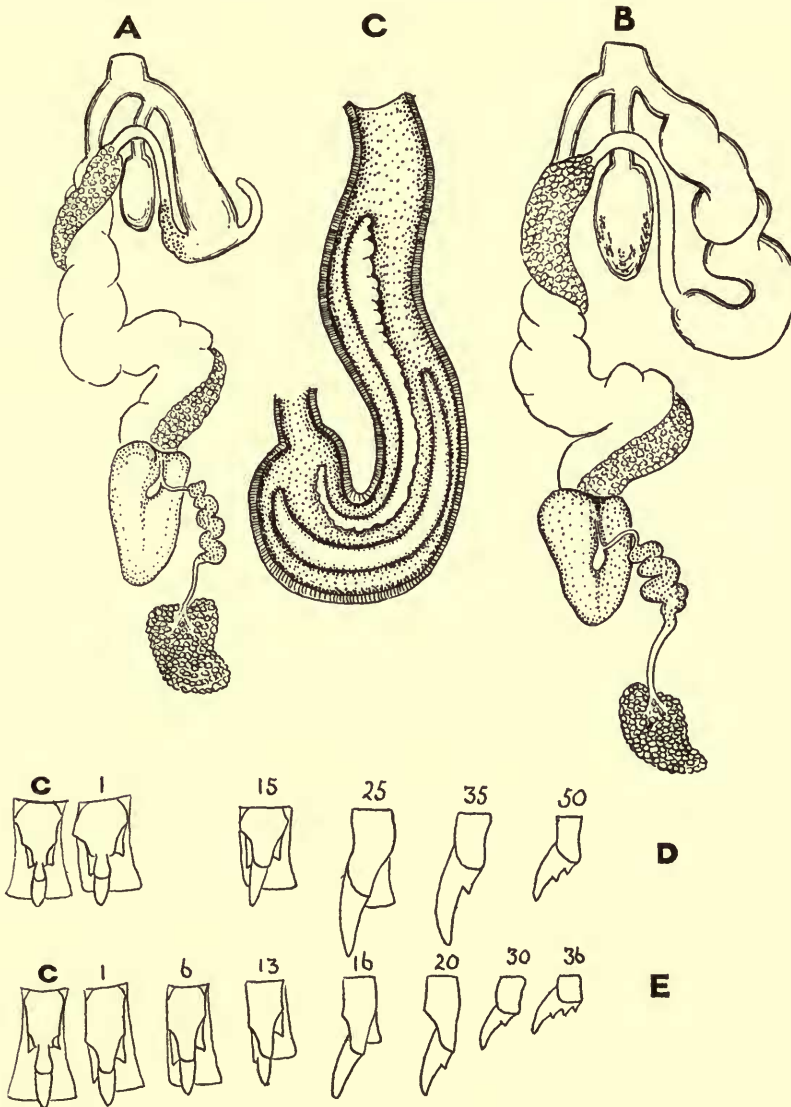


FIG. 17. Greenhouse aliens. A. *Lehmannia poirieri*—genital organs ( $\times 3.3$ ). B. *Limax nyctelius*—genital organs ( $\times 3.3$ ). C. *L. nyctelius*—penis ( $\times 6.7$ ) opened longitudinally. D. *L. poirieri*—representative radular teeth ( $\times 330$ ). E. *L. nyctelius*—representative radular teeth ( $\times 330$ ).

*Mating, development*

No observations on mating seem to have been recorded. Eggs laid in captivity at Swansea in December 1939 were translucent yellow and measured  $2.25 \times 1.5$  mm. They hatched in February. In March the young measured 10.0 mm long, and had intensely black body and mantle bands, and by 10th June they were full grown.

*Ecology*

Found always on the ground, never climbing trees and plants like *L. marginata*. This is true in Tenerife (Altena, 1950) and California (Gregg, *in litt.*), and in a greenhouse at Swansea, where the species was always found under pots.

*Distribution*

Spain, the Canary Isles (? introduced), and introduced into California and Britain (known from greenhouses in Reading, Swansea and Belfast).

*Material examined*

Living specimens taken from a greenhouse in Singleton Park, Swansea, Glamorgan, in 1936, 1938 and 1949; and from a Reading University greenhouse at Shinfield, Reading, in 1959. Spirit specimens from Verdugo Woodlands, Glendale, California (collected by Dr. W. O. Gregg); Güejar de la Sierra, Provincia de Granada, South Spain, and Elizondon, Navarre, North Spain (collected by Dr. de Zarate) and Barcelona.

*Limax nyctelius* Bourguignat, 1861

*Limax nyctelius* Bourguignat, 1861 : 305, pl. 2, figs. 3 and 4. Algeria.

*First British record*

By Quick (1949 : 25). However, A. R. Waterston had found it some years before this, and partially described the species in an unpublished thesis.

*Diagnostic features*

Externally like *Lehmannia poirieri*, and with a similar radula. Internally resembles *L. flavus* in having a long rectal caecum, and a long cylindrical penis without an appendix.

*External appearance*

*L. nyctelius* is about 5 cm long, pale greyish-yellow with a thin translucent body-wall. There is a short inconspicuous keel at the hinder end. The mantle bands form a lyre-shaped figure, and the narrow body bands are high up on each side near the mid-dorsal line. The respiratory orifice has a pale border, and the sole is uniformly pale.

*External variation*

The mantle and body bands vary somewhat in breadth and intensity. Like those of *Lehmannia poirieri*, they tend to fade in alcohol.

*Jaw*

Dark brown or blackish, 1.7 mm across.

*Radula* (Text-fig. 17 E)

A tri-cuspid median tooth is flanked on each side by thirteen to fifteen tri-cuspid laterals and from twenty-eight to thirty aculeate marginals. The marginals beyond about the nineteenth are bifid, and the extreme marginals trifid.

*Alimentary system*

As in *L. flavus*, with two forwardly-directed loops and a long rectal caecum.

*Reproductive system* (Text-fig. 17 B)

The pigmented ovotestis is exposed between the right and left lobes of the liver. The pigmented hermaphrodite duct becomes swollen and folded in its central portion, and ends at the large albumen gland with a pale oval seminal vesicle. The free oviduct is short and stout. The spermatheca arises by a wide duct from the atrium, which expands abruptly to an oval sac which may be pigmented. The penis is uniformly cylindrical, more or less folded, and the vas deferens enters its apex under cover of the stout penial retractor muscle, which arises from the diaphragm close behind the kidney. Internally the penis (Text-fig. 17 C) resembles that of *L. flavus* in containing a prominent fold starting at the apex and expanding below to a "comb", and another shorter smooth fold.

*Ecology*

Recorded from greenhouses and garden frames in Britain, on date palms in Washington, D.C., and beneath flower pots in Egypt (Abu Teira, *in litt.*).

*Distribution*

North African coast and Egypt. Introduced into Britain (known from greenhouses in Edinburgh and Glasgow), North America (known from Washington, D.C.) and South Africa (Connolly 1939 : 176).

*Material examined*

Spirit specimens from the Royal Botanic Gardens, Edinburgh (sent by A. R. Waterston), Shebin El Kom, Egypt, Algeria and Washington, D.C.



## FOSSIL SPECIES

*Limax modioliformis* Sandberger, 1880

*Limax modioliformis* Sandberger, 1880 : 103, pl. xii, figs. 15–15 c.

Fossil shells ascribed to this species are found in the Cromerian at West Runton, Norfolk (Sandberger, 1880). However, the specific ascription of fossil slug shells is at best only tentative. Similar shells in the same beds are ascribed to *Lehmannia marginata*.

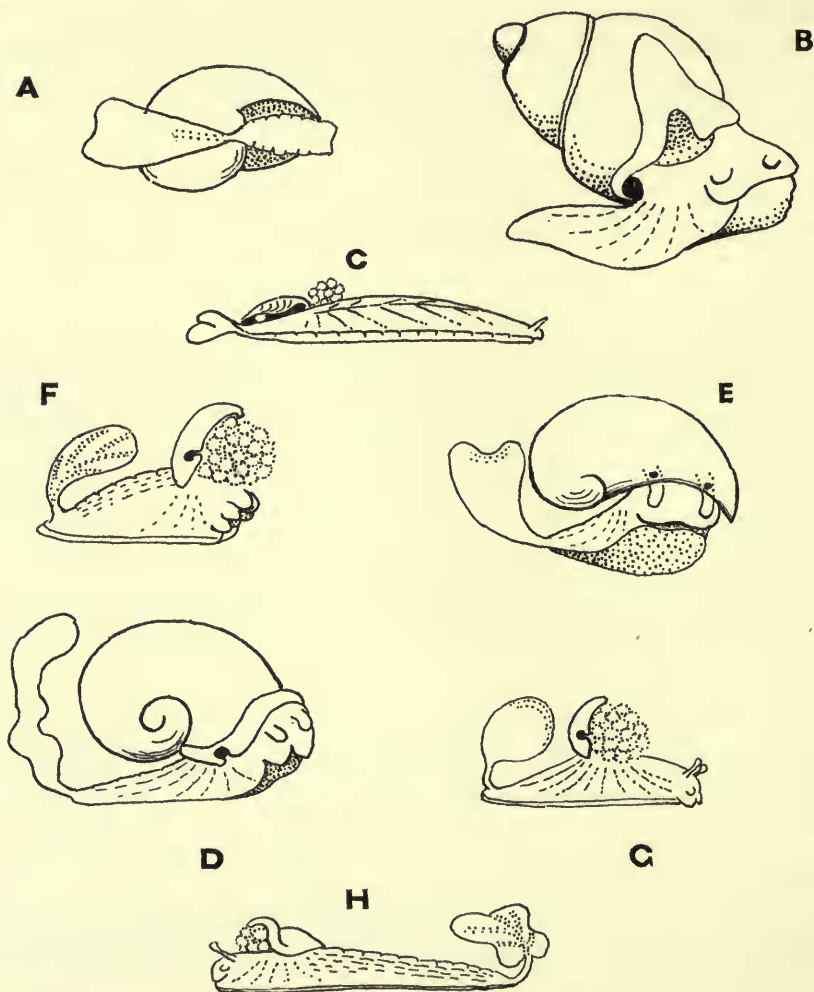


FIG. 18. Embryonic vesicles. A. *Achatina fulica*—embryo ( $\times 6.7$ ) showing large caudal vesicle. B. *A. fulica*—later embryo ( $\times 6.7$ ) with vesicle adsorbed. C. *Testacella scutulum*—embryo ( $\times 6.7$ ) showing cephalic and caudal vesicles. D. *Helix aspersa*—embryo ( $\times 13$ ) showing caudal vesicle, cephalic vesicle adsorbed. E. *Helicella itala*—embryo ( $\times 20$ ) showing caudal vesicle, cephalic vesicle adsorbed. F. *Arion ater*—embryo ( $\times 17$ ) three weeks after laying, with cephalic and caudal vesicles. G. *Agriolimax caruanae*—embryo ( $\times 17$ ) with cephalic and caudal vesicles. H. *Limax cinereoniger*—embryo ( $\times 6.7$ ) with cephalic and caudal vesicles.

## ANATOMICAL TERMS

The following terms are used throughout this paper, in discussing the genital anatomy of slugs. They are illustrated by somewhat generalized illustrations in Text-fig. 19.

<i>Ovotestis</i>	.	.	The hermaphrodite gonad, far back in the visceral mass, producing ova and spermatozoa.
<i>Hermaphrodite duct</i>	.	.	The slender duct conveying ova and spermatozoa from the ovotestis to the albumen gland, oviduct and prostate.
<i>Seminal vesicle</i>	.	.	A loop, enlargement or diverticulum of the hermaphrodite duct at the albumen gland, for the storage of the animal's spermatozoa.
<i>Albumen gland</i>	.	.	A more or less linguiform gland at the termination of the hermaphrodite duct, supplying the egg albumen.
<i>Fertilization sac</i>	.	.	A cavity at the commencement of the oviduct where the ova are fertilized by the partner's spermatozoa.
<i>Prostate</i>	.	.	Glandular tubules, opening into the male duct or groove which conveys the spermatozoa.
<i>Sperm-oviduct</i>	.	.	The combined prostate, male duct or groove and oviduct. The prostate usually appears as a yellow ribbon on the gelatinous-looking oviduct. In the Stylommatophora, the proximal parts of the male and female tracts are not completely separate from one another.
<i>Vas deferens</i>	.	.	The slender male duct after it becomes separate and leaves the sperm-oviduct.
<i>Free oviduct</i>	.	.	The female duct, beyond the point where the vas deferens leaves it.
<i>Spermatheca</i>	.	.	The expanded termination of the spermatheca duct, which arises near the termination of the free oviduct ( <i>Milax</i> ) or directly from the atrium ( <i>Arion</i> , <i>Limax</i> and <i>Agriolimax</i> ). The spermatheca temporarily stores the partner's spermatozoa.
<i>Vagina</i>	.	.	The part of the free oviduct between the origin of the spermatheca duct and the atrium. When the spermatheca duct arises directly from the atrium, there is no vagina.
<i>Atrium</i>	.	.	The terminal portion of the genital ducts, receiving the oviduct, penis and often the spermatheca duct.
<i>Epiphallus</i>	.	.	The enlarged terminal portion of the vas deferens, which secretes the spermatophore and leads to the penis.
<i>Spermatophore</i>	.	.	A chitinous capsule containing a mass of spermatozoa ( <i>Arion</i> , <i>Milax</i> ).
<i>Penis</i>	.	.	The terminal evaginable portion of the male duct, leading to the atrium, and sometimes ( <i>Milax</i> ) containing a penial papilla.
<i>Retractor penis muscle</i>	.	.	A muscle arising from the body-wall and inserted between the epiphallus (when one is present) and the proximal end or apex of the penis. In <i>Arion</i> a penis and retractor are not present; the epiphallus enters the atrium direct, and a retractor muscle is inserted on the free oviduct and the spermathecal duct.
<i>Flagellum</i>	.	.	A slender tubular diverticulum from the apex of the penis ( <i>Testacella</i> ).
<i>Penial appendix</i>	.	.	A conical or digitiform appendage of the penis ( <i>Lehmannia</i> ), or a more or less branched appendage at the apex of the penis ( <i>Agriolimax</i> ).
<i>Sarcobelum</i>	.	.	A stimulatory organ situated in the penis ( <i>Agriolimax</i> ).
<i>Stimulator</i>	.	.	A stimulatory organ situated in the atrium ( <i>Milax</i> ).
<i>Ligula</i>	.	.	A lobulated or frilled mass in the atrium or lower part of the oviduct in <i>Arion</i> , which in copula functions as an adhesive organ between the partners.
<i>Vaginal glands</i>	.	.	A mass of glandular tubules in <i>Milax</i> , discharging into the termination of the oviduct and the atrium.

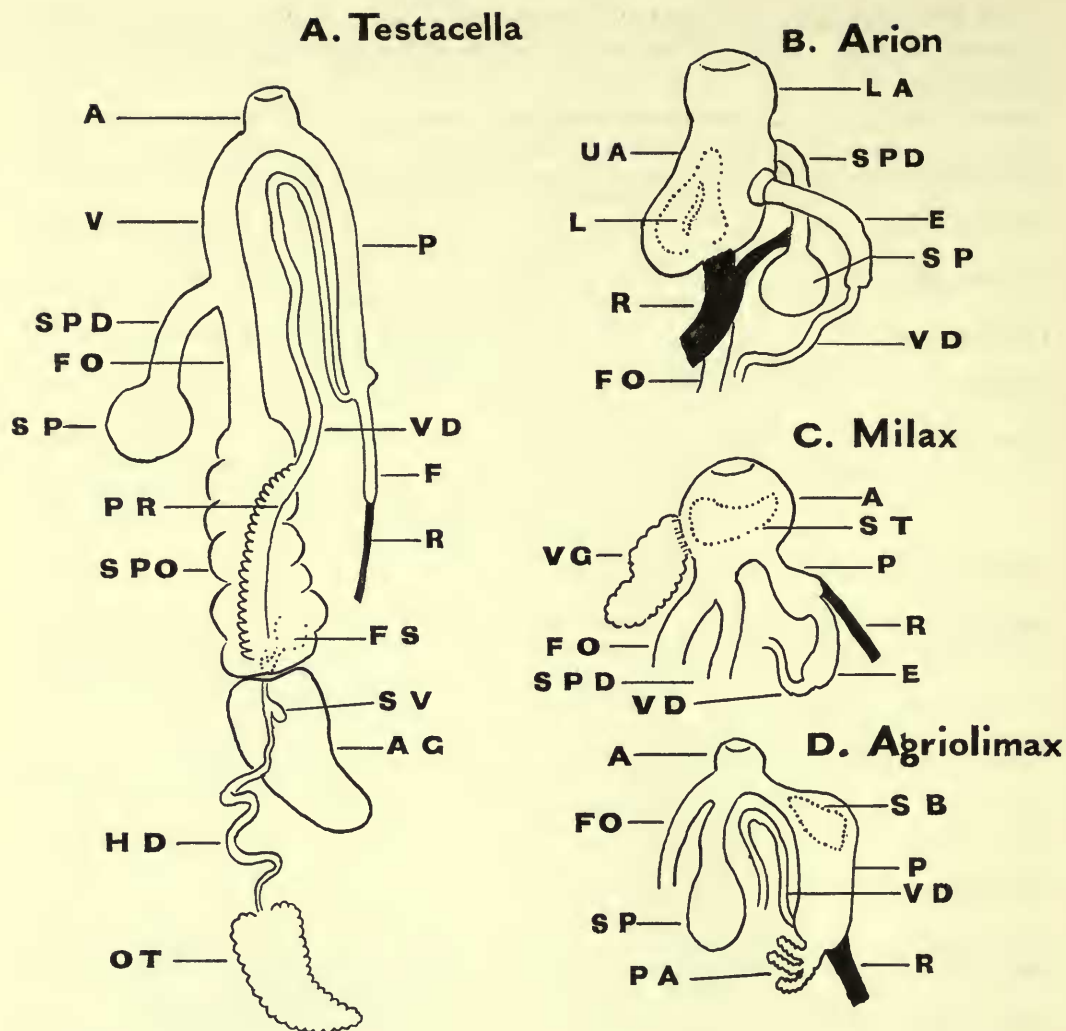


FIG. 19. Genital anatomy. A. *Testacella*. B. *Arion*. C. *Milax*. D. *Agriolimax*.

Key : A—atrium  
 AG—albumen gland  
 E—epiphallus  
 F—flagellum  
 FO—free oviduct  
 FS—fertilization sac  
 HD—hermaphrodite duct  
 L—ligula  
 LA—lower atrium  
 OT—ovotestis  
 P—penis  
 PA—penial appendix

PR—prostate  
 R—retractor muscle  
 SB—sarcobelum  
 SP—spermatheca  
 SPD—spermatheca duct  
 SPO—spermoviduct  
 ST—stimulator  
 SV—seminal vesicle  
 UA—upper atrium  
 V—vagina  
 VD—vas deferens  
 VG—vaginal glands.

## DISTRIBUTION

The numeration of vice-counties adopted in the following maps is that of Druce (1932) and the *New Naturalist* series, not that of the Conchological Society Census (Ellis, 1951). In citing vice-counties by numbers, the Irish series should be prefixed by "H".

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Channel Isles  
PENINSULA

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MAP 3.—Distribution of *Testacella scutulum* in Britain.MAP 2.—Distribution of *Testacella haliotidea* in Britain.



MAP 5.—Distribution of *Arion intermedius* in Britain.MAP 4.—Distribution of *Geomalacus maculosus* in Britain.

MAP 7.—Distribution of *Arion hortensis* in Britain.MAP 6.—Distribution of *Arion fasciatus* in Britain.

MAP. 9.—Distribution of *Arion lusitanicus* in Britain.MAP 8.—Distribution of *Arion subfuscus* in Britain.



MAP 11.—Distribution of *Arion ater rufus* in Britain.MAP 10.—Distribution of *Arion ater ater* in Britain.

MAP 13.—Distribution of *Milax sowerbyi* in Britain.MAP 12.—Distribution of *Milax gagates* in Britain.





MAP 15.—Distribution of *Agriolimax reticulatus* in Britain.



MAP 14.—Distribution of *Milax budapestensis* in Britain.

MAP 17.—Distribution of *Agriolimax laevis* in Britain.MAP 16.—Distribution of *Agriolimax agrestis* in Britain.

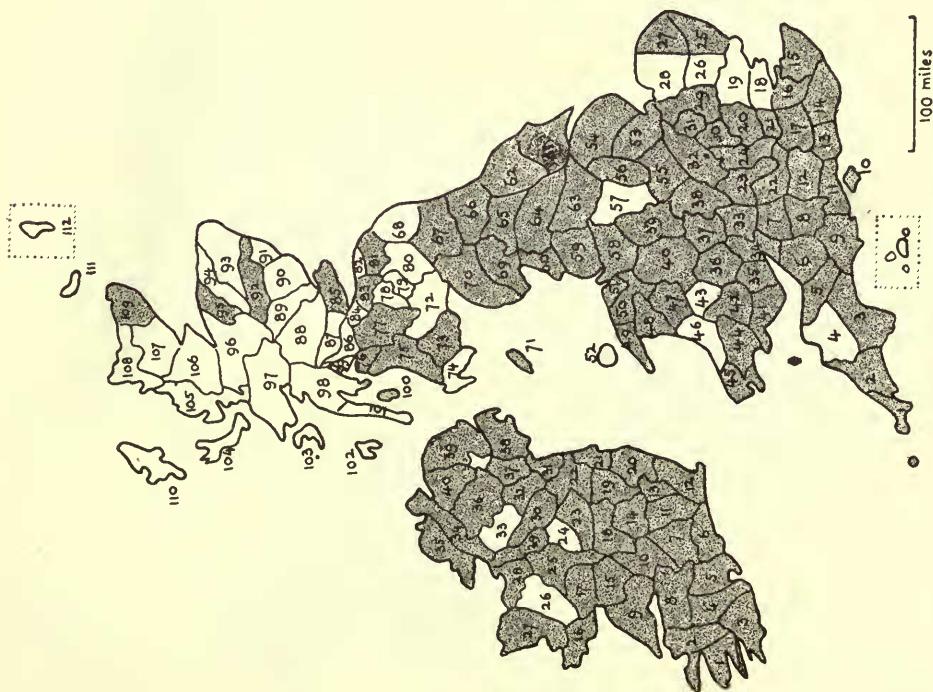


MAP. 19.—Distribution of *Limax tenellus* in Britain.



MAP 18.—Distribution of *Agriolimax caruanae* in Britain. New records from Ireland need to be added: Cork Mid. (H<sub>4</sub>) and Down (H<sub>38</sub>).



MAP. 21.—Distribution of *Limax cinereoniger* in Britain.MAP. 20.—Distribution of *Limax flavus* in Britain.



MAP 23.—Distribution of *Lehmannia marginata* in Britain.



MAP 22.—Distribution of *Limax maximus* in Britain.



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## PLATE I

The scale lines represent one centimetre.

- |                                       |  |  |
|---------------------------------------|--|--|
| 1. <i>Geomalacus maculosus</i> .      | 3. <i>Arion ater ater</i> .                  | 2. <i>Arion subfuscus</i> .                |
| 4. <i>Arion hortensis</i> .           | 7. <i>Arion intermedius</i><br>(contracted). | 5. <i>Arion fasciatus</i> .                |
| 6. <i>Arion intermedius</i> .         | 10. <i>Testacella haliotideae</i> .          | 8. <i>Arion fasciatus</i><br>(contracted). |
| 9. <i>Arion subfuscus</i><br>(young). | 12. <i>Milax gagates</i><br>(contracted).    | 11. <i>Arion ater rufus</i><br>(young).    |
| 13. <i>Testacella maugei</i> .        |  | 14. <i>Lehmannia poirieri</i> .            |

